ISSN 0082–3449

CONTRIBUTIONS IN MARINE SCIENCE

VOLUME 30 DECEMBER 1987

CONTRIBUTIONS IN MARINE SCIENCE

VOLUME 30 DECEMBER 1987

PUBLISHED BY

MARINE SCIENCE INSTITUTE
THE UNIVERSITY OF TEXAS AT AUSTIN
PORT ARANSAS, TEXAS 78373-1267

FOUNDED BY E. J. LUND IN 1945

Editor: Donald E. Wohlschlag
Editorial Assistant: Rebecca Ford
Technical Editor: Ruth Grundy

CONTRIBUTIONS IN MARINE SCIENCE (Formerly *Publications of the Institute of Marine Science*) is printed at irregular intervals by The Marine Science Institute and includes papers of basic or regional importance in marine science, with emphasis on the Gulf of Mexico and surrounding areas.

Issues are distributed at a cost of $8.00 per copy (no discounts possible), or on an exchange basis.

Reprints of individual articles are distributed through the authors only.

For orders (Volumes 7 onward plus three supplements are available), further information, or exchange arrangements please write to the Librarian, Marine Science Institute, The University of Texas at Austin, Port Aransas, Texas 78373-1267. Prospective contributors should consult the Instructions to Authors included in this volume.

Copyright © 1988

INSTRUCTIONS TO AUTHORS

1. Manuscripts should be sent to The Editor, *Contributions in Marine Science*, The University of Texas at Austin, Marine Science Institute, Port Aransas, Texas 78373-1267. Manuscripts may be submitted on any aspect of marine science. Preference is given to papers relating to the Gulf of Mexico and presenting the results of original research. Papers describing new methods will also be considered. Reviews may be published but authors should consult with the editor before submitting a manuscript. Reviews will normally be considered from workers active in the field reviewed. Short notes are usually unsuitable.

   Papers will be returned to the authors for revision if the style and presentation do not conform to the journal's convention.

   All contributions are sent to outside reviewers for evaluation of scientific merit and reader interest.
2. The submission of a manuscript will be taken to imply that it has not already been published nor is being considered for publication and if accepted by *Contributions in Marine Science* that it will not be published elsewhere.
3. Manuscripts must be typewritten in English with double spacing throughout (text, literature cited, table and figure headings).
4. Page one of the manuscript should give the title in capitals, the author's name and the address(es) where the work was carried out. Footnotes may be used on the title page to indicate present addresses of authors, but should be avoided in the text. Also indicated on page one should be a short title of not more than 60 letters and spaces for use as a page heading.
5. Page two should contain an abstract. This should be concise and intelligible without the need to refer to the text.
6. The introduction should start on page three. The major headings (ABSTRACT, INTRODUCTION AND METHODS, RESULTS, DISCUSSION) should be capitalized and centered on the page. For sub-headings, capitalize the initial letter of significant words. The first sub-heading should be centered, the second shouldered and the third run-on with the text.
7. Use metric units instead of or in addition to other units. Authors should consult *Style Manual for Biological Journals*, The American Institute of Biological Sciences, Washington, D.C. for questions of general style and a list of acceptable abbreviations.
8. References in the text may be in the form "Smith (1960)" or "(Smith 1960)". When repeated references are made to papers with more than two authors, give the authors in full the first time and subsequently use the first author followed by *et al.* The full list of authors should be listed under literature cited. When reference is made to a book, the page may be indicated in the text, *e.g.*, (Smith 1960, p. 170).
9. The literature cited should be arranged alphabetically by author(s) and then chronologically, *i.e.*, Smith, A. and Abe, B. 1970, comes before Smith, A. and Brown, A. 1960. The titles of papers and the title of journals should be given in full.
10. References to books should give the editor, date, title, page, publisher's name and place of publication. The following examples illustrate the style to be followed:

    Journal:

    VAN CLEVE, R., R.Y. TING and J.C. KENT. 1966. A new device for sampling marine demersal animals for ecological studies. *Limnology and Oceanography.* **11**:438–443.

    Book:

    HUTCHINSON, J. 1959. *Families of Flowering Plants.* Macmillan, N.Y. 792 pp.

    Thesis:

    HOESE, H.D. 1965. Spawning of marine fishes in the Port Aransas, Texas area as determined by the distribution of young and larvae. Ph.D. Thesis. University of Texas, Austin.

    Chapter:

    PROVASOLI, L. 1963. Organic regulation of phytoplankton fertility, pp. 165–210. In M.N. Hill (ed.) *The Sea, Vol. 2.* Interscience, N.Y.

11. Line drawings on Bristol board or good quality white paper should be drawn large enough for reduction to ½ size. They should not exceed 11 × 8½ inches.
12. Tables should be typed with IBM prestige elite 72 (12 pitch) or an equivalent, single spaced. Use a light italic (12 pitch) rather than underlining. Prepare camera ready copy.
13. Photographs should be on glossy paper. On the back of all illustrations, the name(s) of the author(s), the number of the illustration and an indication of the top edge should be given. Legends to the figures and tables should be typed on a separate sheet of paper.
14. There are no page charges but the high cost of printing may preclude the acceptance of long papers with large numbers of illustrations unless the author can make a contribution to the cost of publication.

CONTENTS

Instructions to Authors iii

Temperature and mixing on the Texas continental shelf
Lauren E. Sahl and William J. Merrell, Jr. 1

Relative selectivity of five coastal
marsh sampling gears ***R.H. Hartman and W. H. Herke*** 17

Organic carbon and nitrogen flow from marine cyanobacteria
to semiaquatic insect food webs
Warren M. Pulich, Jr. and Richard S. Scalan 27

The role of hurricanes in determining year-class strength
of red drum ***Gary C. Matlock*** 39

The vertical distribution and feeding ecology of *Euchaeta marina*
in the eastern Gulf of Mexico ***P.G. Shuert and T.L. Hopkins*** 49

The importance of behavioral and biochemical differences
between fiddler crab taxa, with special reference to *Uca rapax*
(Smith) and *U. virens* (Salmon and Atsaides)
Michael Salmon and Michelle K. Kettler 63

Variability in the distribution of late-stage oyster larvae
in the Calcasieu Estuary ***Michael Vecchione*** 77

Comparison of fruits and seeds of *Syringodium* (Cymodoceaceae)
from Texas, U.S. Virgin Islands, and the Philippines
Louis H. Bragg and Calvin McMillan 91

Recurrence of fruiting by *Halophila engelmannii*
(Hydrocharitaceae) in Redfish Bay, Texas ***Calvin McMillan*** 105

Contributions in Marine Science. (1987) Vol. 30:1–16.

SALINITY, TEMPERATURE AND MIXING ON THE TEXAS CONTINENTAL SHELF

Lauren E. Sahl[1] and William J. Merrell, Jr.[1]

Department of Oceanography
Texas A&M University
College Station, Texas 77843

ABSTRACT

Salinity and temperature data are presented in order to examine variability of Texas shelf hydrography. Data taken during March 1982 show advection of mid-shelf water to the outer shelf. These data also show the interleaving and/or turbulent mixing of shelf and slope waters near the shelf edge. Data from March 1982, May 1982 and November 1982 show that low salinity surface water was present at the shelf edge during most of the year. These data indicate that offshore transport of water by advection is common. Evidence of such advection would eventually be destroyed by shelf-edge processes, such as interleaving or turbulent mixing.

INTRODUCTION

That Mississippi River discharge dominates the salinity of Texas shelf waters has been documented and described by Lewis (1982), Cochrane and Kelly (1986), Smith (1980), and Harrington (1971). The discharge results in a brackish wedge on the inner shelf for much of the year. At the shelf edge low salinity surface water has been observed and is attributed to convergence of shelf waters and resulting offshore transport of coastal water.

All these studies were based on coarse sample spacing, thus outlining general salinity distributions. This study examines East Texas shelf hydrography using close sample spacing, both vertically and horizontally. To our knowledge it is the only such study on the East Texas shelf and reveals features of the hydrography not previously discussed.

METHODS

The study area extends from the coast to the continental shelf edge for that part of the shelf between Matagorda Bay and Galveston Island. Data from three cruises are used to examine the spatial variability and temporal variability of temperature and salinity distributions over the continental shelf.

---

[1] Now at: Texas A&M University at Galveston, Mitchell Campus, P. O. Box 1675, Galveston, Texas 77553

All cruises were conducted aboard the R/V GYRE, operated by Texas A&M University. Cruises were conducted from March 17 to March 22, 1982, from May 3 to May 4, 1982, and from November 15 to 16, 1982. On the March and May cruises the Profiling Hardwired Instrumented Sensor for Hydrography (PHISH) package was the primary instrument used for data acquisition. The PHISH package contains a temperature probe, a pressure sensor, and a conductivity meter. Salinity is calculated from conductivity and temperature measurements using formulae from Lewis (1980). For data within oceanic ranges, the maximum error of these formulae is about 0.0015‰ in salinity. Included in the instrument package are two 5-liter Niskin bottles that are automatically tripped just above the bottom when a weighted line touches the bottom. A more complete description of the PHISH system can be found in McGrail, Carnes, Horne, Cecil, Hawkins and Halper (1982).

On the November cruise a Neil Brown CTD (conductivity, temperature and depth) was deployed at each station. Salinity was determined from conductivity and temperature measurements using the same formulae used to calculate salinities for the PHISH system data. Water samples were taken at the bottom of each cast using a rosette sampler.

Salinity of water samples was determined using a 6230N Grundy Inductive Salinometer. These data were used to check the conductivity sensors. Also, reversing thermometer readings were taken to check the performance of the temperature sensors.

During the March cruise, five distinct sections were occupied. Figure 1 shows the bathymetry of the study area and the location of the stations. Data from these sections were examined to determine the horizontal and vertical variation in the temperature and salinity distributions over the shelf. Stations 1 to 18 comprise section A, 20 to 26 comprise section B, 27 to 31 comprise section C, 32 to 40 comprise section D, and 40 to 45 comprise section E (Figure 1). Vertical sections showing the distribution of temperature, salinity, and σ_t (density) were prepared for all of the sections.

Horizontal distributions of temperature and of salinity are presented at 10 m depth and at the bottom or 26.2 σ_t surface, whichever is shallower. The horizontal surface at 10 m depth is chosen to minimize diurnal effects on the temperature of the surface waters. In order to look at the water flowing along the bottom and then off the shelf along a density interface, temperature and salinity distributions are mapped on the bottom or the 26.2 σ_t surface, whichever is shallower.

RESULTS

Spatial Variation in Hydrography

Horizontal Distributions

The temperature distribution at 10 m depth (Figure 2a) shows that the 20°C and 21°C isotherms on the outer shelf generally parallel the bathymetry, while the 18°C and 19°C isotherms on the mid and inner shelf form a thermal front which is oblique to the shelf bathymetry. In general, this same pattern is evident in the deeper temperature field (Figure 2b). The temperature distribution in Fig. 2b shows a mass of colder water on the midshelf in the northeast section of the study area. At the shelf edge a tongue of colder water is present in the southwest portion of the study area. Figure 2c, which depicts the salinity distribution at 10 m depth, shows that on the inner shelf isohalines are oblique to the bathymetry with a pronounced salinity gradient coinciding with the 18°C front. Indeed, at 10 m depth, both the isotherms and the isohalines wedge into the coastline, implying that colder, fresher water is entering the study area from the northeast. During this time of year (March)

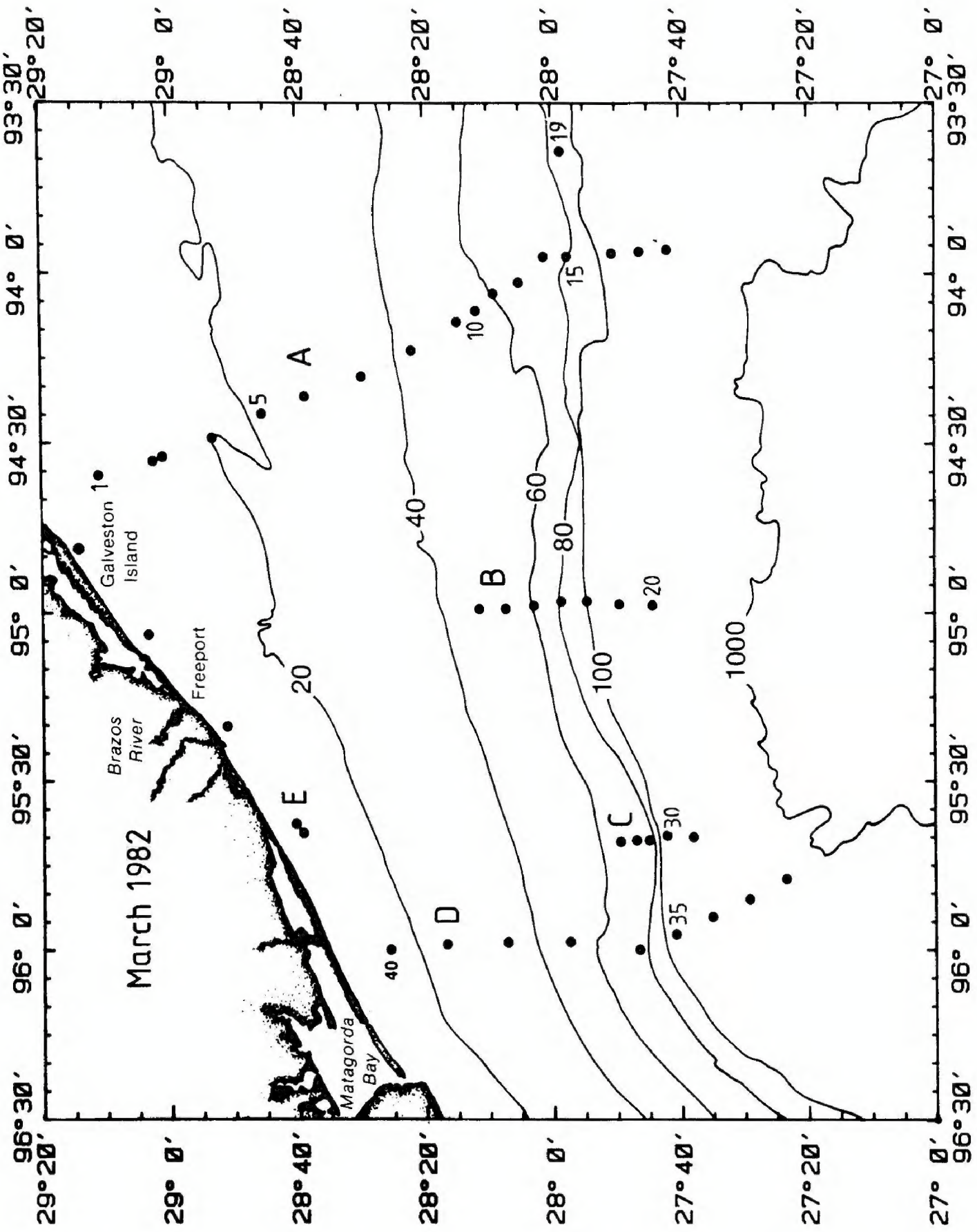


FIG. 1. Station locations for March 1982 cruise. Bathymetry is in meters. Letters A to E indicate sections.

coastal currents are usually to the southwest and carry fresher water from the Mississippi and Atchafalaya outflow (Kelly and Randall 1980). Near the shelf edge a tongue of fresher water entering the study area from the west is indicated in the 10 m depth salinity field (Fig. 2c). This tongue is also evident

in the near bottom salinity field (Fig. 2d). The near bottom temperature field (Fig. 2b) shows that this low salinity tongue is relatively cold. The tongue is at least 60 km long in the near surface waters and 100 km long near the bottom. The tongue of water must have an onshore source since it is both fresher and colder than the surrounding waters. This implies that inner or mid-shelf

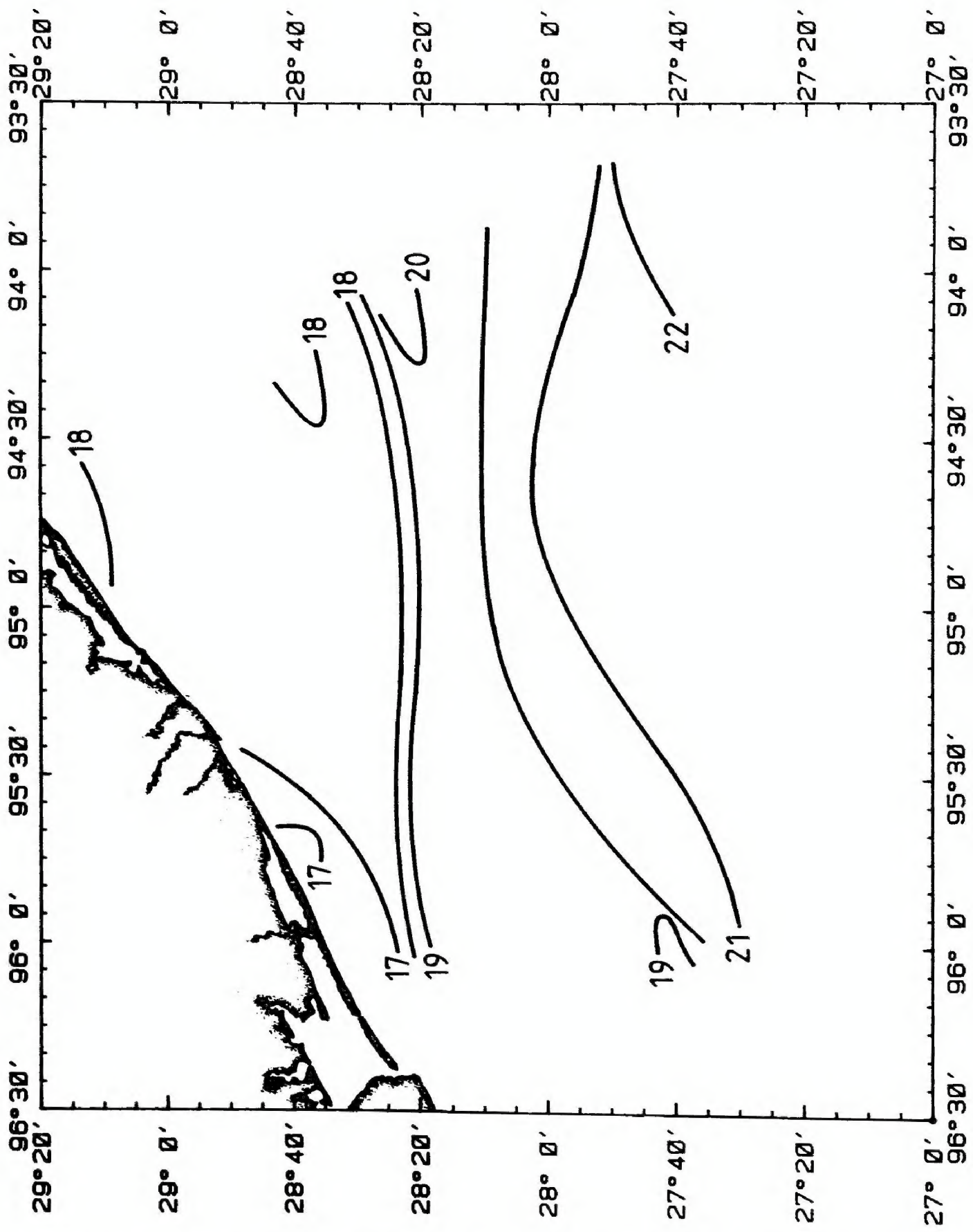


FIG. 2A. Horizontal distribution of temperature at 10 m depth in March 1982. Contour interval is 1°C.

waters have been advected offshore. Measuring the distance (in section D) between the nearshore 36‰ isohaline (at 10 m depth) and the 36‰ isohaline near station 37 we calculate an offshore displacement (not necessarily a trajectory) of about 40 km. Considering that the shelf width in the study area varies from 86 to 174 km this cold, fresh tongue is a major feature.

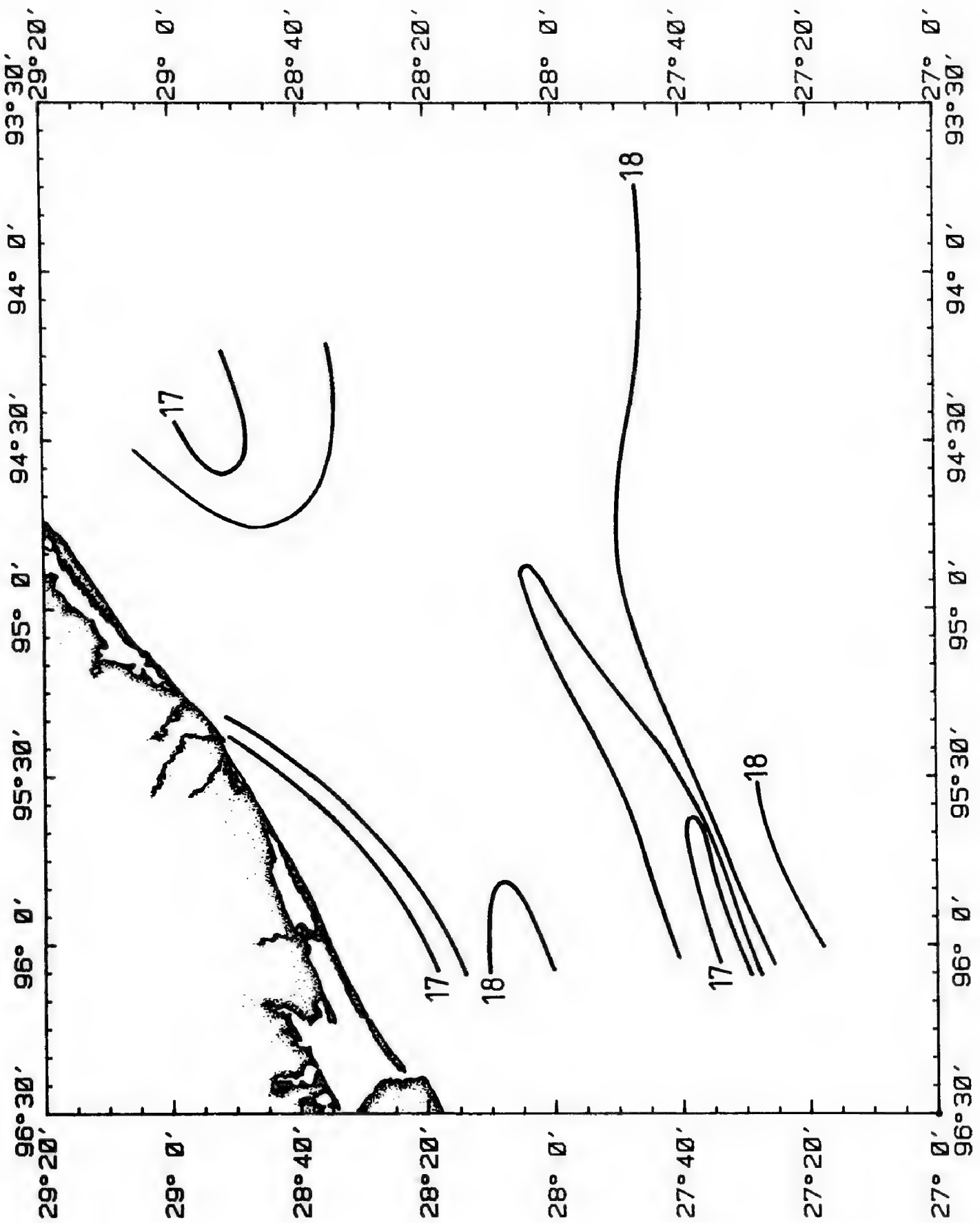


FIG. 2B. Horizontal distribution of temperature at the sea-bottom or on the 26.2 σ_t surface, whichever is shallower, in March 1982. Contour interval is 0.5°C.

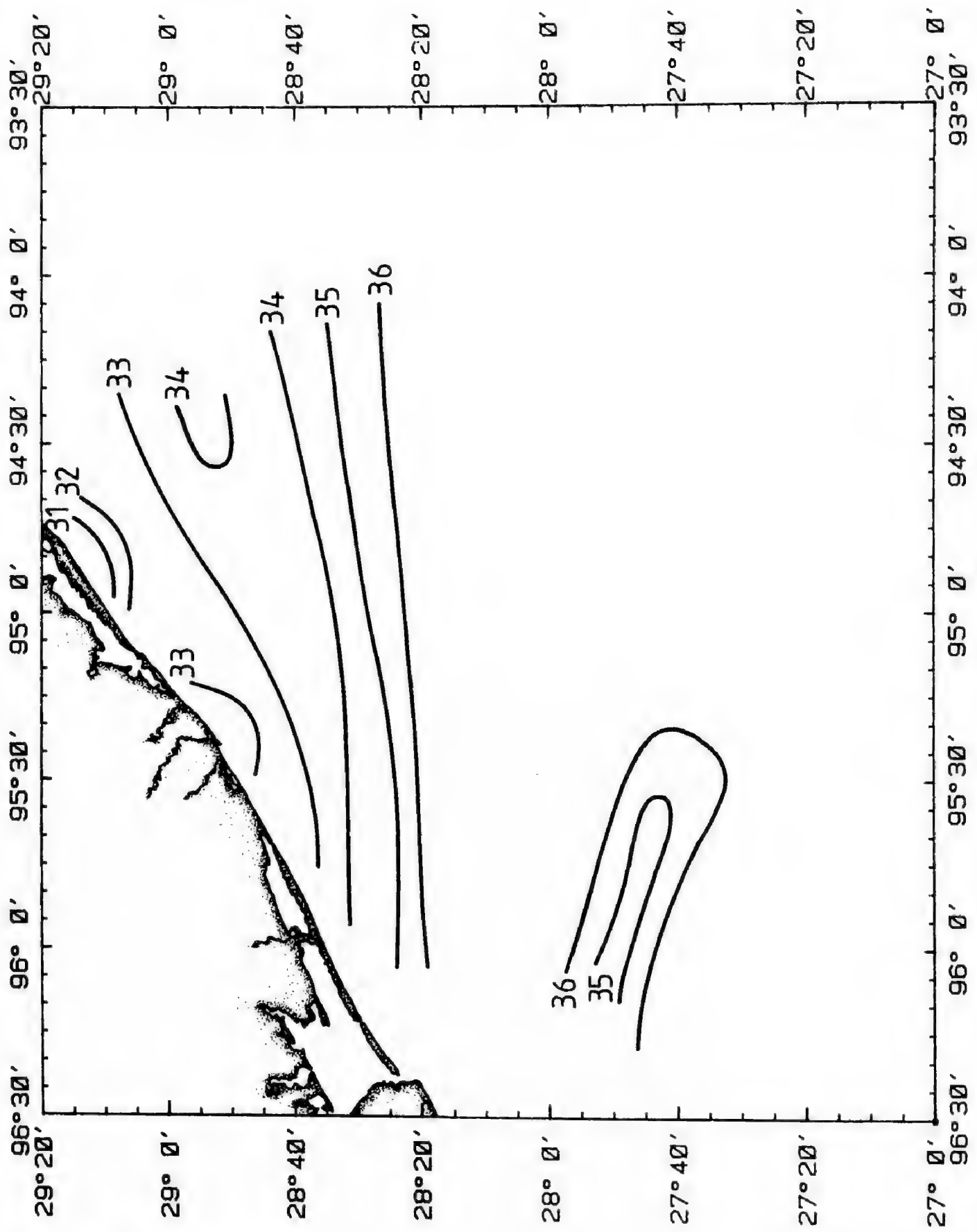


FIG. 2C. Horizontal distribution of salinity at 10 m depth in March 1982. Contour interval is 1‰.

Cross-shelf Hydrography

Vertical sections of the cross-shelf hydrography are noteworthy in the detail depicted. The general form confirms what is known of seasonal Texas shelf

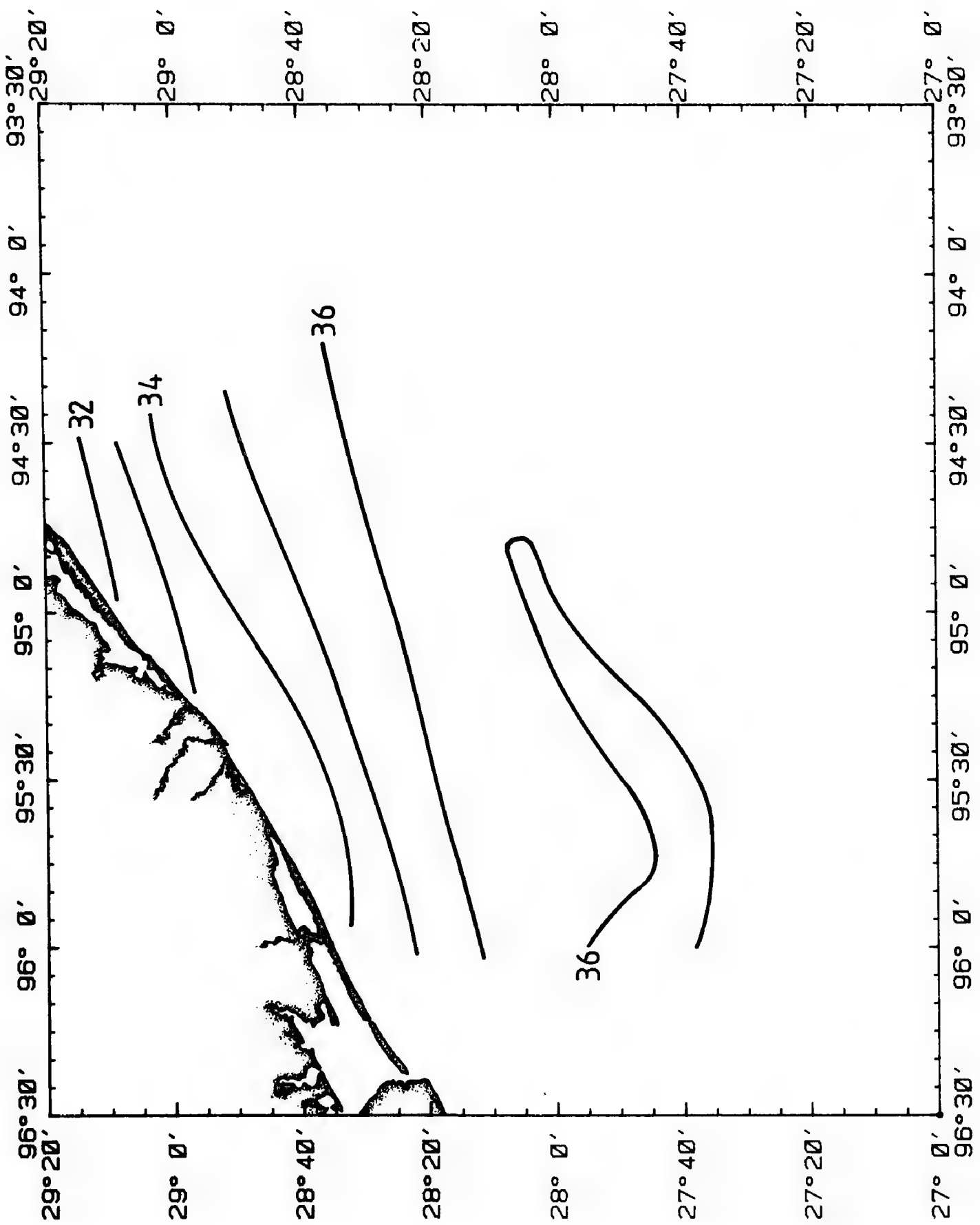


FIG. 2D. Horizontal distribution of salinity at the sea-bottom or on the 26.2 σ_t surface, whichever is shallower, in March 1982. Contour interval is 1‰.

hydrography, with the low salinity water near the coast controlling the water density there. Temperatures increase offshore and at this time of the year there is no well developed thermocline over the shelf or slope (Sahl 1984). Figures 3a and 3b show the salinity distributions for the two cross-shelf

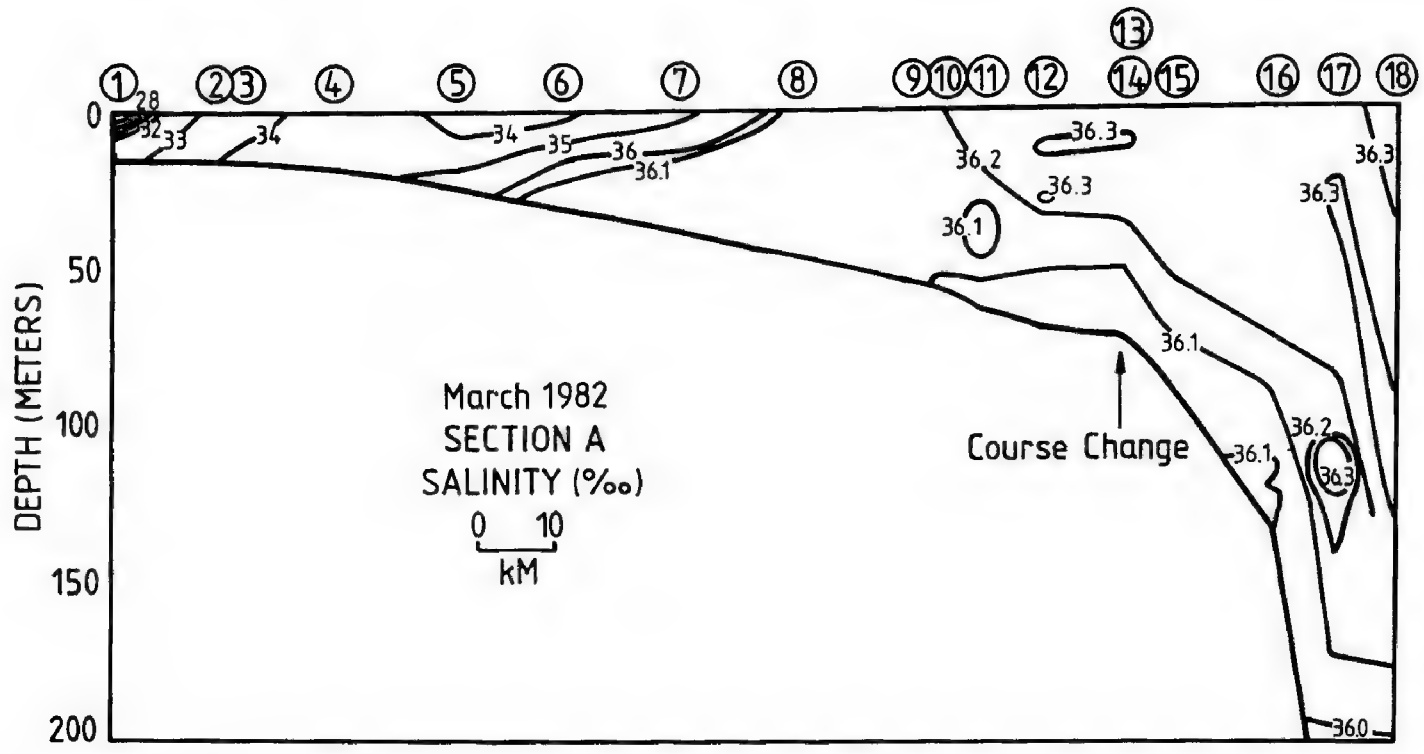


FIG. 3A. Vertical section of salinity, section A, March 1982. Contour interval over outer shelf and slope is 0.1‰. Over the midshelf the contour interval is 1.0‰. On the inner shelf the contour interval varies, note the marked values of the contour lines. Circled numbers are station locations.

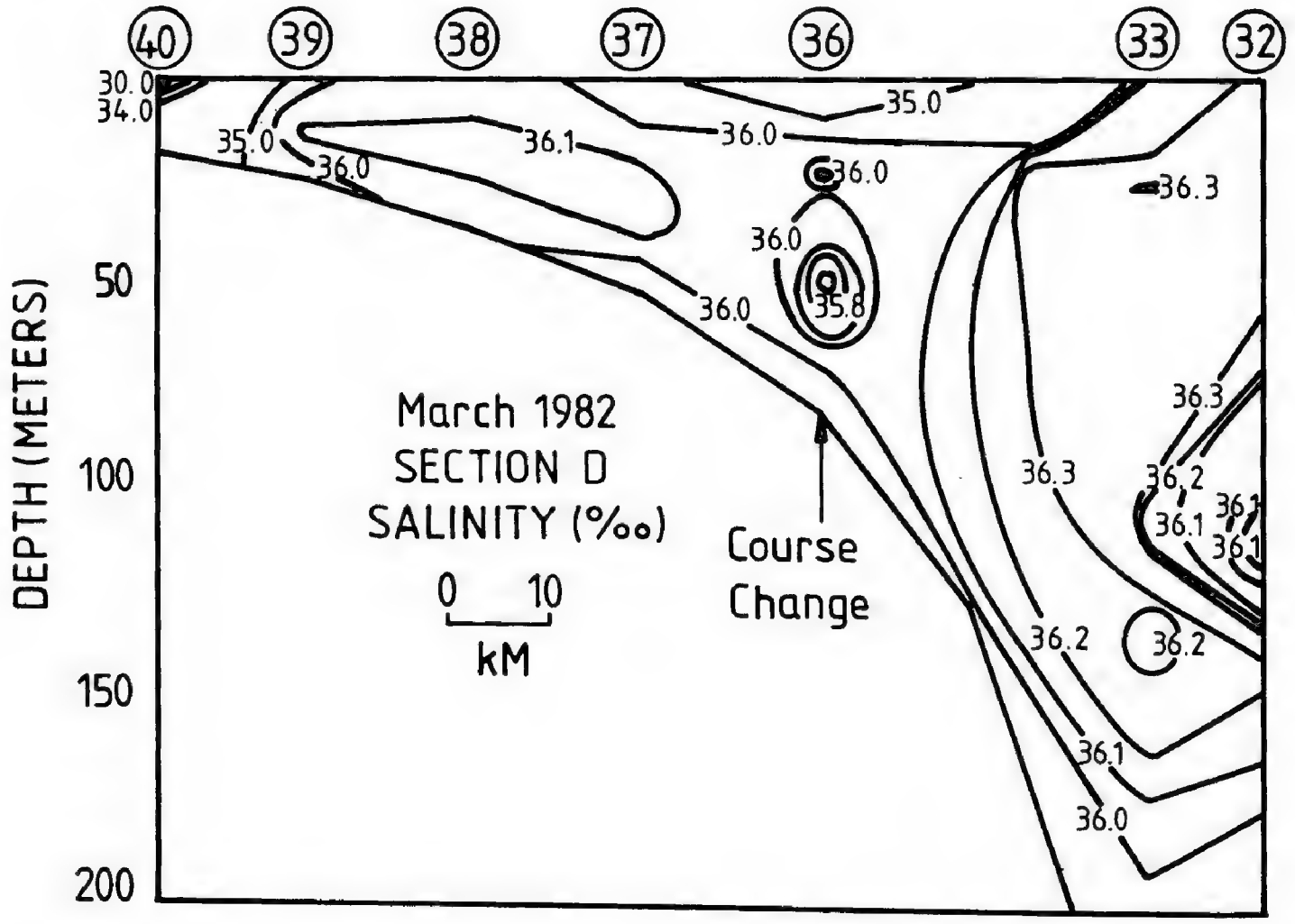


FIG. 3B. Vertical section of salinity, section D, March 1982. Contour interval varies so note the marked values of the contour lines. Note there are no stations 34 and 35. Data from these two stations are not available due to CTD malfunction.

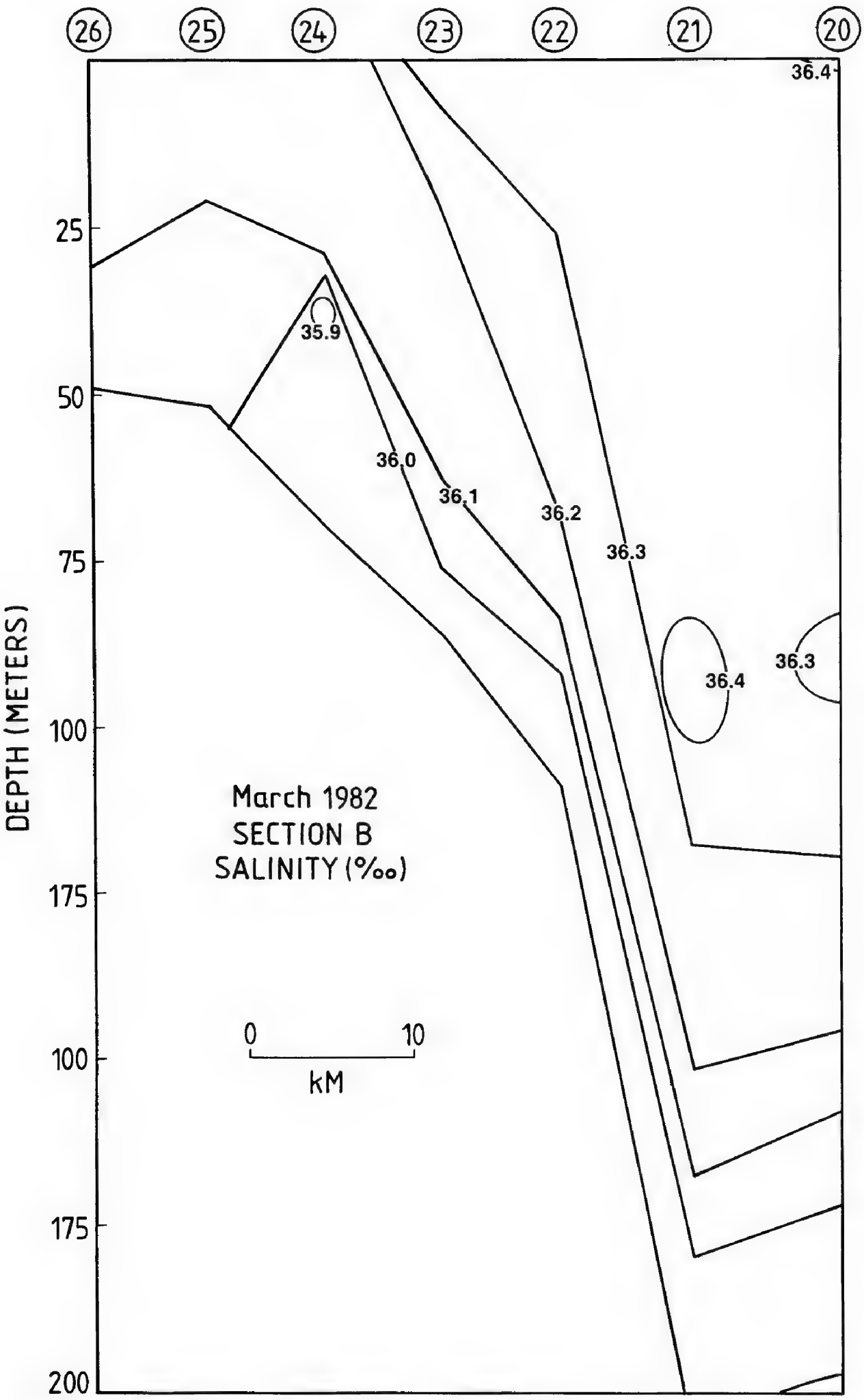
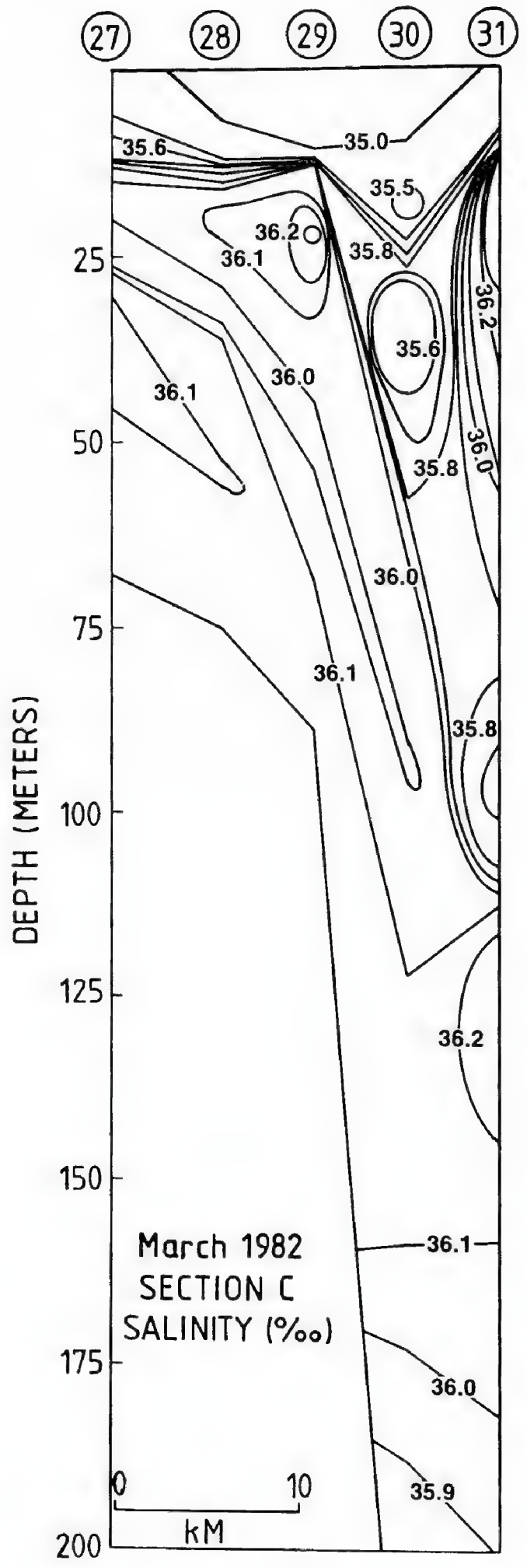


FIG. 4A-B. Vertical section of salinity for March 1982, a) section B, b) section C. The contour interval of section C varies due to high gradients. Note the marked values of the contour lines.



sections, A and D. The salinity distributions show that the fresher water on the inner shelf may extend at least halfway across the shelf, as in section A. The

salinity front that bounds this brackish wedge usually slopes down towards the shore, but section D (Fig. 3b) shows that this need not be the case. Offshore transport of bottom water has resulted in a bending of the salinity front. Present at the shelf edge in both sections are small scale (ten's of meters thick) high and low salinity lenses. Similar structures are not present in the temperature field.

Sections B and C are across the shelf edge only. The salinity distributions for these sections are shown in Figs. 4a and b. The salinity field for section C (Fig. 4b) shows great complexity due to small scale lenses of high and low salinity. The lenses in section C vary in thickness, reaching a maximum of approximately 50 m. Section B (Fig. 4a) is much less complicated. To examine these lenses further, T-S diagrams were drawn for a station with a minimum of small scale structures, station 21 (Fig. 5a) and for two stations with small scale structures, 30 and 31 (Figs. 5b and 5c).

Figure 5a is the T-S diagram for station 21 from the surface to 200 m. The salinity change for this depth range is 0.5‰. Waters from 0-90 m are most saline. Below 90 m salinities decrease with increasing depth. Temperatures decrease with increasing depth. This T-S distribution is for shelf-edge waters unaffected by inner or mid-shelf intrusions. On the other hand, T-S distributions for stations 30 and 31 clearly show the effects of mid-shelf water intrusions (Figs. 5b and 5c). Below 150 m at station 30 and 130 m at station 31 the T-S distribution is very like that of station 21. But above these depths the water column is affected by interfingering and/or mixing of waters with different T-S signatures. Both stations have the same gross form, a relatively straight sloping section, "a bulge", then the straight sloping section that begins at 130-150 m. The straight sloping section at the top in both cases is due to the fresher tongue of surface water previously discussed. At depth the effects of this fresher water mixing with slope waters are shown in the sections of the T-S diagrams that bulge. Figure 4b shows that some of this mixing is occurring in the form of interleaving indicated by the salinity highs and lows in the section.

Temporal Variation in Hydrography

On the May and November cruises a section running north-south along longitude 95° west was occupied. These data can be used to examine temporal variability of the Texas shelf hydrography.

Station locations are shown in Fig. 6 for these two cruises. Fig. 1 shows the station locations for the March cruise, during which section B was occupied along 95° west. Salinity data from the two later cruises are shown in Fig. 7.

As is typical for the spring, a brackish wedge is present on the inner shelf in May (Fig. 7a). A halocline has developed over the outer shelf and slope, and at the same depth a thermocline is present (not shown). Both the temperature (not shown) and salinity fields indicate mixing of shelf waters for November (Fig. 7b) with steeply dipping contour lines. This winter mixing is typical of

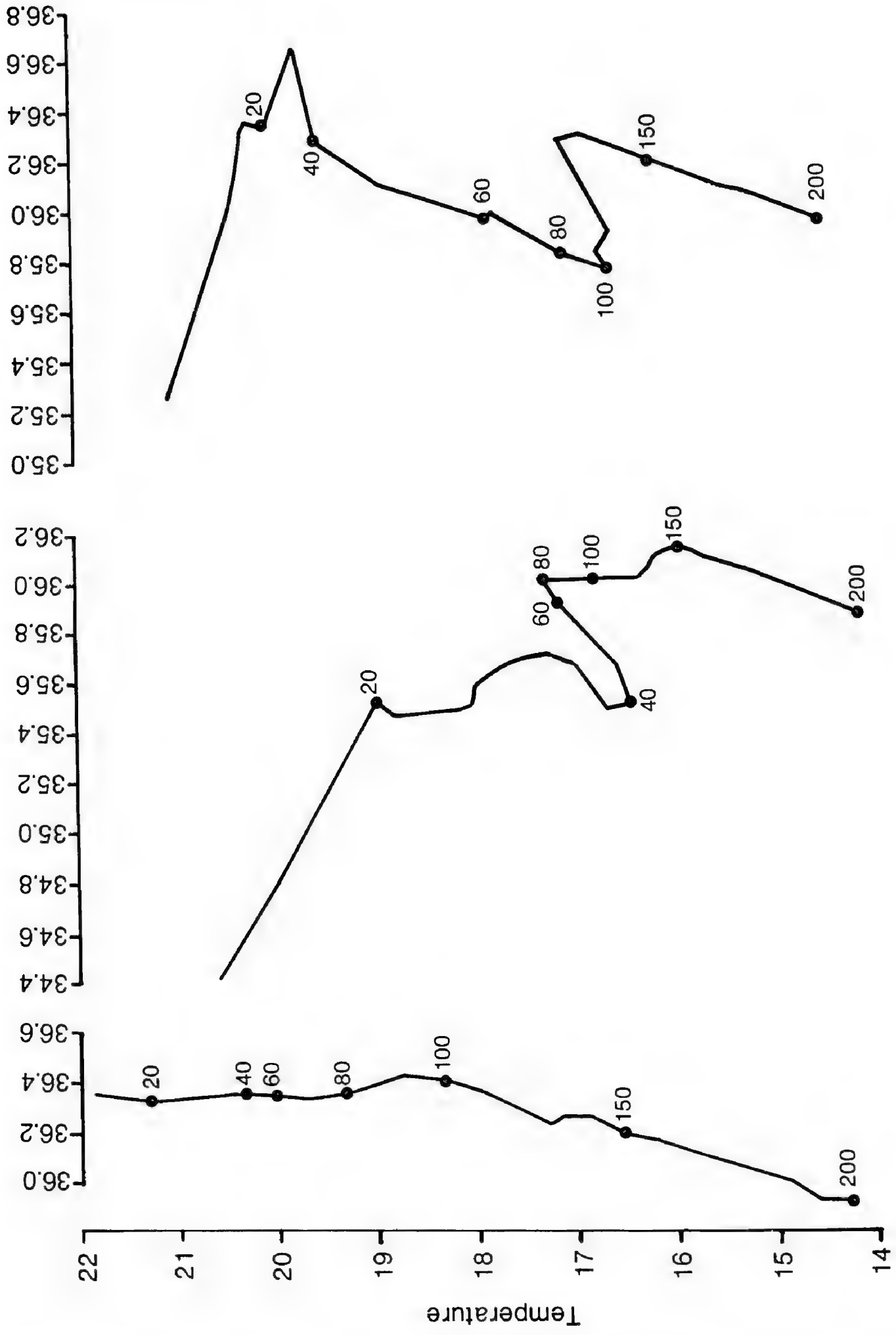


FIG. 5A-C. Temperature *versus* salinity for a) station 21, b) station 30, and c) station 31, March 1982. The depth, in meters, is marked by dots.

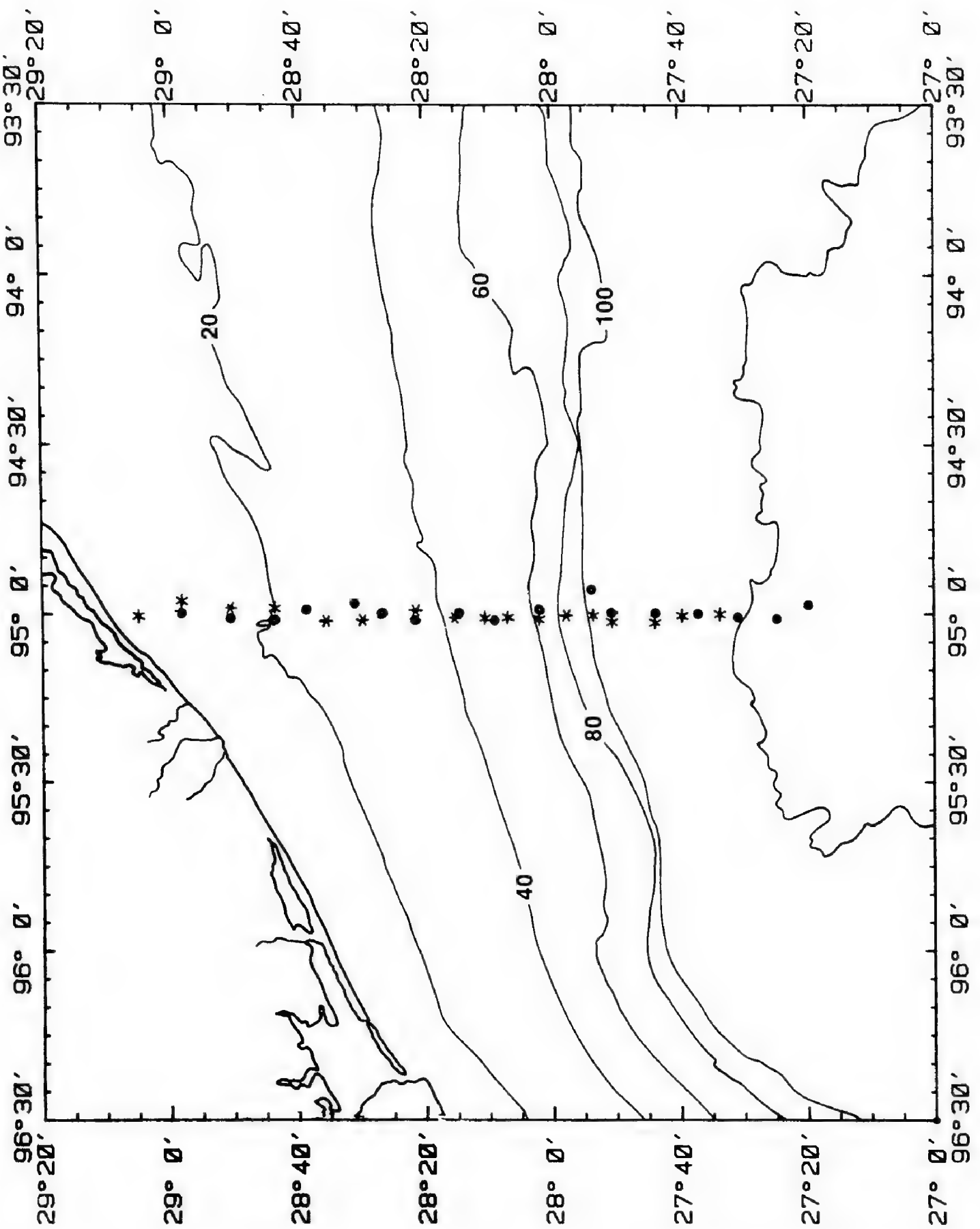


FIG. 6. Station locations for May 1984 cruise (dots) and November 1984 cruise (stars).

the Texas shelf. Significantly, both sections show relatively fresh surface water over the continental slope, though the waters are not as fresh as those observed in March. No small scale features are present in the salinity field, as are present in the March data set. These data argue that fresher water at the shelf edge is not uncommon.

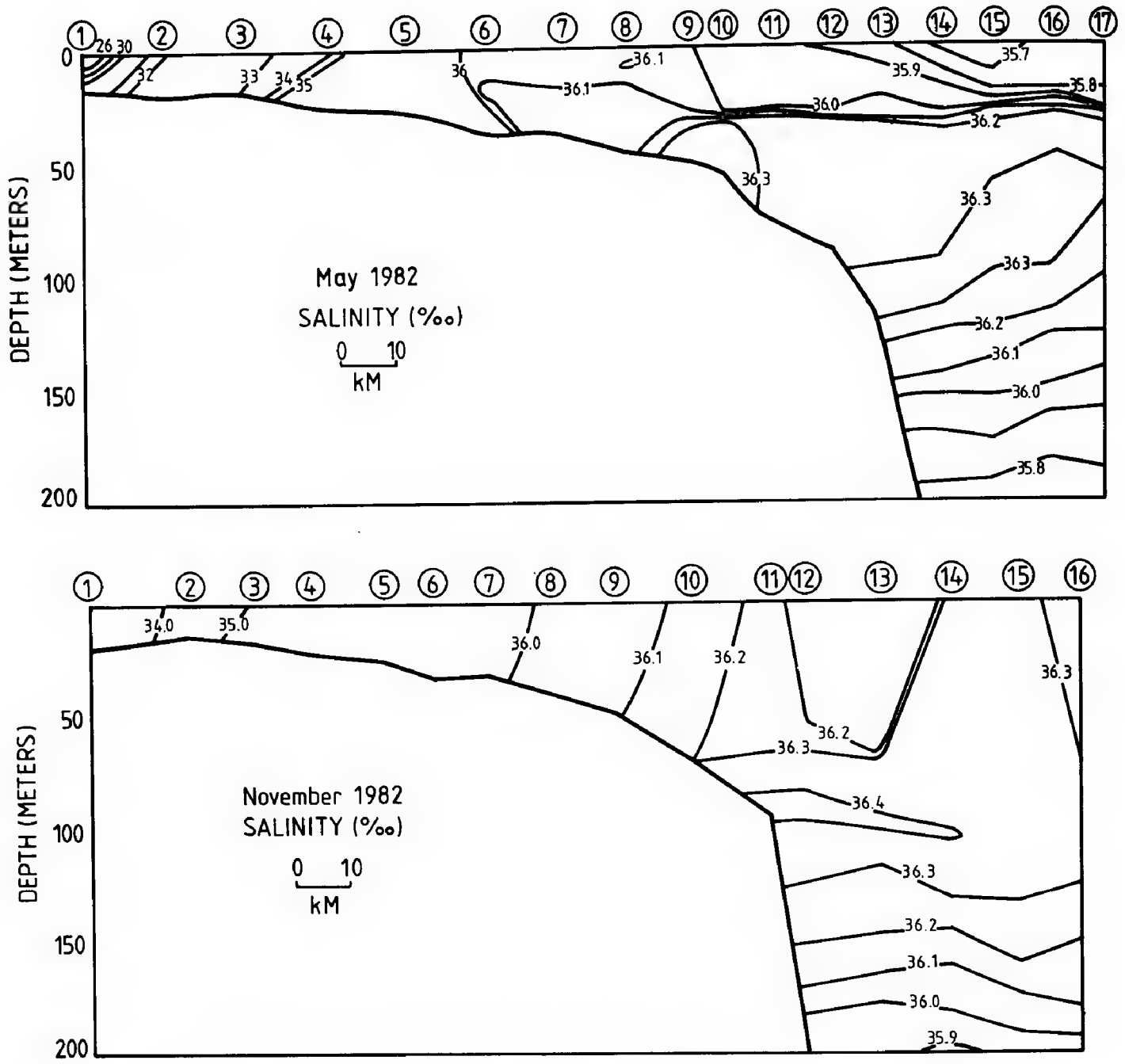


FIG. 7A-B. Vertical sections of salinity for a) May 1982, b) November 1982. Contour interval varies so note the marked values of the contour lines.

DISCUSSION

Although inner shelf circulation on the Texas shelf is well known, the circulation of the mid and outer shelf is not well understood. Inner shelf currents are to the southwest for much of the year, driven by the alongshore wind component. These currents carry river runoff, creating the brackish wedge on the inner shelf. Cochrane and Kelly (1986) summarize present knowledge on Texas shelf circulation and postulate cyclonic circulation on the Texas-Louisiana shelf for much of the year. The southern limb of the cyclone is on the Texas shelf and results in offshore transport. Over the shelf edge currents are directed eastward. This type of circulation would result in low salinity inner and mid-shelf water being carried out over the shelf edge. The data we present here show evidence of such offshore transport. Moreover we are able to resolve much smaller spatial scales than those presented in

Cochrane and Kelly (1986). The seasonal surface salinity pattern they present shows low salinity water over the slope from May through July. Data presented here show this phenomena may start as early as March. The phenomena observed here may be on a smaller scale than that reported in Cochrane and Kelly (1986). They postulate a gyre covering the whole shelf. The salinity pattern observed here could also be explained by an eddy on the East Texas shelf, or an advected bolus of inner shelf water. The observed pattern may occur in conjunction with larger scale phenomena, such as a gyre, and add to the complexity of the general circulation.

If the salinity pattern reported here is part of the cyclone, we were fortunate in March 1982 to sample the eastward limit of the low salinity shelf-edge water. Sections C and D (Figs. 4b and 3b) document low salinity water, A and B (Figs. 3a and 4a) do not. Between sections B and C the low salinity water has mixed with shelfedge water. The fine-structure in the salinity data (Figs. 3b and 4b) is evidence of turbulent mixing and/or interleaving. Similar features have been observed by Wright (1976) and Miller (1950) on the New England shelf. The T-S pattern for the mixing we observe is similar to that observed by Gregg (1975) off the coast of California. This T-S pattern is caused by interleaving of different water masses, in this case inner or mid-shelf waters with slope water. The interleaving would lead to small scale mixing until eventually the shelf waters would be indistinguishable at the shelf edge. These fine-structured features would be transitory, so it is not surprising that we do not observe them on all cruises.

These data then present new insight into Texas shelf circulation. At times inner and mid-shelf water is advected to the outer shelf. At the shelf edge this water and slope water mix and/or interleave, producing a complex T-S pattern. Diffusion and turbulence eventually destroy the direct evidence of shelf waters.

This study reveals that close sampling, vertically and horizontally, is necessary for Texas shelf hydrographic investigations. Our one meter vertical spacing seems to be sufficient, but close as our horizontal spacing is, it is not close enough. Most of the lenses observed in the salinity and temperature data were documented at only one station. This argues for closer station spacing in shelf hydrography investigations.

ACKNOWLEDGMENTS

This work was funded partially by the Minerals Management Service (Department of the Interior) and the Sea Grant College Program (National Oceanographic and Atmospheric Administration). Shiptime was provided by the State of Texas through Texas A&M University. One of the authors (Sahl) had a National Aeronautics and Space Administration Traineeship during the course of the study. We also acknowledge the excellent support of the captain and crew of the R/V GYRE and of the Department of Oceanography's technical services group. Finally, we appreciate the encouragement and help of our many colleagues—especially Dr. David McGrail.

LITERATURE CITED

COCHRANE, J.D. and F.J. KELLY. 1982. Proposed annual progression in the mean Texas-Louisiana shelf circulation (abstract). *EOS.* **63(45)**:1012.

_____ and _____. 1986. Low-frequency circulation on the Texas-Louisiana continental shelf. *Journal of Geophysical Research.* **91(9)**:10,645-10,659.

GREGG, M.C. 1975. Microstructure and intrusions in the California current. *Journal of Physical Oceanography.* **5**:253-278.

HARRINGTON, D.L. 1971. Oceanographic observations on the northwest continental shelf of the Gulf of Mexico, 1963-65. Unpublished manuscript. 25 p.

KELLY, F.J. and R.E. RANDALL. 1980. Physical oceanography. In R.W. Hann and R.E. Randall (eds) *Evaluation of Brine Disposal from the Bryan Mound Site of the Strategic Petroleum Reserve Program.* Department of Energy, Strategic Petroleum Reserve Project Management Office.

LEWIS, E.B. 1980. The practical salinity scale 1978 and its antecedents. *IEEE Journal of Ocean Engineering.* **OE-55**:3-8.

LEWIS, J.K. 1982. On the nearshore hydrography of the Upper Texas coast. PhD Thesis. Texas A&M University, College Station.

McGRAIL, D., M. CARNES, D. HORNE, T. CECIL, J. HAWKINS, and F. HALPER. 1982. Water and sediment dynamics at the Flower Garden Banks. In *Environmental Studies at the Flower Gardens and Selected Banks: Northwestern Gulf of Mexico, 1979-1981.* Technical Report 82-7-T, Texas A&M Research Foundation, Texas A&M University, College Station.

MILLER, A.R. 1950. A study of mixing processes over the edge of the continental shelf. *Journal of Marine Research.* **9**:145-159.

SAHL, L.E. 1984. Suspended sediment on the upper Texas continental shelf. PhD Thesis. Texas A&M University , College Station.

SMITH, N.P. 1980. On the hydrography of shelf waters off the central Texas Gulf coast. *Journal of Physical Oceanography.* **10**:806-813.

WRIGHT, W.R. 1976. The limits of shelf water south of Cape Cod, 1941 to 1972. *Journal of Marine Research.* **34**:1-14.

Contributions in Marine Science. (1987) Vol. 30:17–26.

RELATIVE SELECTIVITY OF FIVE COASTAL MARSH SAMPLING GEARS

R. D. Hartman and W. H. Herke

Louisiana Cooperative Fish and Wildlife Research Unit[1]
School of Forestry, Wildlife and Fisheries
Louisiana State University Agricultural Center
Baton Rouge, Louisiana 70803

ABSTRACT

Two otter trawls (1.8-m and 4.8-m), two push trawls of differing widths (2.1-m and 4.2-m), and a 57-m long-haul seine were evaluated for sampling fishes and crustaceans in a shallow coastal marsh of southwest Louisiana. Ease of use, number of species captured, and number of organisms per 1000 m^2 of surface area sampled were compared for each sampling gear. Although the otter trawls were easiest to use, they yielded the lowest density of organisms for most species. The wide push trawl was the most expensive and cumbersome gear, but yielded the highest number of organisms/1000 m^2. The long-haul seine was the most difficult gear to use, but captured the most species, the most species per sample, and generally the most organisms per sample.

INTRODUCTION

Gear selectivity is produced by any characteristic which causes a gear to capture a non-representative sample of a population (Kushlan 1974). Many techniques for sampling shallow coastal marshes are selective in one way or another. Perry (1978) compared an otter trawl to rotenone for sampling a Louisiana marsh and reported the former to yield a biased representation of the community. Weinstein and Davis (1980) compared rotenone with a seine; both methods yielded representative samples of the nekton community although rotenone showed a non-significant, but higher, species richness.

Selectivity and gear efficiency are directly related. Selectivity is an expression of the difference in numbers or length frequency captured by a sampling gear from what is actually present in the water body (Backiel and Welcomme 1980). Efficiency is the percentage of organisms in the path of a gear that is captured (Kjelson and Johnson 1978). Efficiency of a 4.9-m otter trawl was estimated by Loesch, Bishop, Crowe, Kuckyr and Wagner (1976) for *Penaeus aztecus* (45%), *Micropogonias undulatus* (25%), and *Leiostomus xanthurus* (6%). Kjelson and Johnson (1978) found higher catch efficiencies for *Leiostomus xanthurus* (32%) using a larger trawl (6.1-m). Watson (1976) reported

[1] The Unit is supported by Louisiana State University Agricultural Center, Louisiana Department of Wildlife and Fisheries, and the U.S. Fish and Wildlife Service.

mean catch efficiencies for penaeid shrimp using 15-m and 21-m electrical otter trawls of 54% and 35% respectively. Macketts (1973) and Kjelson and Colby (1977) determined catch efficiencies of 3.0-m, 4.6-m and 6.1-m otter trawls for several common marsh fishes. Relative efficiencies were greater for the largest trawl.

Selectivity and efficiency of the various sampling gears used in shallow coastal marshes must be quantified to yield the best possible estimates of such important population characteristics as stock size, recruitment and diversity. Improved knowledge of the selectivity and efficiency of, and the problems inherent in, each gear should help fisheries biologists choose the sampling gear that best meets their needs. Towards this end we compared two widths of otter trawls, two widths of push trawls and a long-haul seine for ease of use, number of species captured, and number of individuals captured/1000 m^2 sampled.

MATERIALS AND METHODS

Sample Collection

Sabine National Wildlife Refuge in southwestern Louisiana fits the description of brackish marshes provided by Chabreck (1972). Four stations were sampled: two deep stations, averaging 47 and 45 cm deep, and two shallow stations, averaging 19 and 24 cm deep. All stations were open-water areas and all sampling gears were used in the same sections of each station.

Sampling began 19 April 1982 and ended 31 July 1982. The study was divided into eight 2-week periods during which each of the sampling gears was used once at every station during each period. Thirty two samples were taken with each gear. The five sampling gears were:

1) 57-m long-haul seine
2) 1.8-m otter trawl
3) 4.9-m otter trawl
4) 2.1-m surface push trawl
5) 4.2-m surface push trawl.

Trawl dimensions and mesh sizes of the push and otter trawls conformed to the gear specifications of similar nets commonly used in estuarine studies in Louisiana (Hartman 1984). A long-haul seine is not commonly used in Louisiana, so its mesh size was chosen to approximate the mesh of the trawls.

The long-haul seine was 57 m long and 1.2 m deep with a 4.8-mm woven delta-type mesh. The seine was used in a manner similar to that described by Kjelson and Johnson (1974). A bag 1 m deep with an opening 1.2 m × 1.0 m was situated at one end of the seine. The other end was fixed to an otter trawl board, which was attached by a 23-m rope to the airboat. The bag end of the seine was attached to a stationary, vertical post to fix that end of the net in an upright position. The net was deployed in a straight line as the airboat was pushed away from the post. The seine was thus stretched in a straight line between the airboat and the post before sampling began. The airboat was moved in a circular direction until it was 90° from the beginning position; it was then turned to draw the net across the post and pulled so that the net stayed against the post until only a small enclosure containing the capture organisms remained at the bag end of the seine. The lead lines of the enclosure were then pinched together and the whole end was lifted onto the airboat deck. The average area fished was 1700 m^2.

The push and otter trawls were used for five minutes each at 2000 rpm (maximum safe rpm's for our airboat). Average velocity for all trawls was determined by using each for five minutes in a canal that ran parallel to a road. Distance traveled was then measured and divided by the elapsed time to determine velocity. The mean value of five repetitions was used. Surface area fished by each gear was determined by multiplying the distance traveled in five minutes by the mouth opening of each gear.

The 4.9-m otter trawl consisted of a 16-mm bar mesh body and a 6.3-mm bar mesh tail. Each otter trawl board measured 40 by 76 cm and was attached by a 23-m line to a bridle slung underneath the airboat. Average velocity was 1.35 m/s. With a mouth width of 2.5 m (Loesch *et al.* 1976), the surface area fished by this trawl was 1012 m^2.

The 1.8-m otter trawl had an 8-mm bar mesh body and 4.8-mm bar mesh tail. The otter trawl boards measured 25 by 46 cm. It was fished in the same manner as the larger trawl except at a velocity of 1.8 m/s. With a mouth width of 1.35 m (field measurement), the surface area fished was 729 m^2.

Both push trawl nets had a 6.3-mm bar mesh body and a 3.2-mm bar mesh tail (Hartman 1984). The single push trawl net was attached to a rectangular hollow aluminum frame 2.1 m wide and was adjusted to fish from the surface to just above the bottom. It was pushed by the airboat for 5 minutes at a speed of 1.8 m/s. The total surface area sampled was 1140 m^2.

The double push trawl (Herke 1969) was similar to the single push trawl but fished an area twice as wide. It was pushed for 5 minutes at a speed of 1.2 m/s, and sampled 1567 m^2.

The long-haul seine and otter trawls were used at all stations on the same day. One week later both push trawls were used at all stations. Order of use of each gear at each station was rotated so that the use of one gear would not continually bias the catch of another.

All samples taken with each gear were placed in individual mesh bags and preserved in a cooler containing ice and water. All fish and crustaceans were sorted to species, counted and measured. Fish standard length, shrimp total length and crab carapace width were measured in 5-mm increments. For example, all organisms measuring 20 to 24 mm were assigned to the 20 mm length class.

Data Analysis

The variance among gears in the number of species captured per sample was tested with a split-plot model analysis of variance (Steele and Torrie 1980) using SAS (1985) procedures. PROC GLM was used to help correct for unbalanced data. This model used Type II sums of Squares with gear and station as main effects. The design blocked on period and utilized interactions as error terms. Duncan's Multiple Range Test (Steele and Torrie 1980) pinpointed significantly different ($P < 0.05$) variance among gear types.

The number captured/1000 m^2 was log transformed (log (number/1000 m^2 + 1)) to help correct for non-normality of distribution and these numbers were tested in the same split-plot analysis of variance design described above. All zero catches were included in the analysis. Duncan's Multiple Range Test pinpointed significant differences in numbers captured among gear types.

RESULTS

Over 138,000 fishes and crustaceans representing 47 species were captured during the study. *Brevoortia patronus* dominated the catch and *Anchoa mitchilli* was second overall. Over half of the total catch by numbers was made up of these two species. The next most numerous species captured were three euryhaline forms; *Cyprinodon variegatus, Palaemonetes* sp. and *Poecilia latipinna.*

The effects of various mesh sizes on numbers captured appeared small. The large otter trawl had a tail mesh width only 3.0 mm greater than the smallest mesh, which was in the tails of the push trawls, and the mesh size of all other gears varied by no more than 1.6 mm. Few individuals less than 24 mm were captured by any gear during the first six periods of the study (Table 1). Data from the final two periods were not used in this table because the 4.9-m otter trawl was not used at all shallow stations during this time.

A greater percentage of the catch of the 4.9-m otter trawl (having the largest

TABLE 1

Percentage catch of each gear in selected length classes during the first six sampling periods.

Length class (mm)	Gear: Long-haul Seine	Push Trawls: single	Push Trawls: double	Otter Trawls: 1.8-m	Otter Trawls: 4.9-m
0-14	0.0	0.0	0.0	1.3	0.5
15-19	0.1	0.1	0.2	1.9	0.6
20-24	1.6	0.8	1.8	3.6	1.5
25-29	8.6	10.9	21.1	9.5	7.5
30-34	28.2	15.5	36.5	28.6	15.2
35-39	32.2	22.9	18.6	16.7	14.1
40-44	19.7	27.0	9.8	9.6	17.9
45-49	5.2	2.0	4.5	5.7	9.7
50-74	2.9	7.1	3.3	12.2	12.2
75-99	1.0	1.9	2.8	8.4	15.6
100+	0.2	1.2	0.8	1.9	4.7

mesh) was composed of fish less than 20-mm standard length, which was greater than all other gears except the 1.8-m otter trawl (Table 1). Both otter trawls captured greater percentages of large organisms than the other gears (Table 1).

Each gear was compared using three criteria: 1) ease of use, 2) number of different species captured, and 3) number captured/1000 m^2 fished.

Ease of Use

Although each gear required only one person, two people operated all gears more efficiently. Clear differences in effort and time were required to sample a station with each gear. The long-haul seine required by far the most; about an hour was required to set and retrieve the seine, remove all organisms, and reload the net onto the boat. Seine samples with large amounts of small fish and debris took up to 1.5 hours to finish. A sampling run with either push trawl averaged 25 minutes from start to finish, while an otter trawl sample involved the least effort and only required approximately 15 minutes.

Some negative aspects were found for each gear. The otter boards of the 4.9-m trawl had a tendency to fall over in water less than 20 cm deep, making shallow water sampling with this gear impossible. The depth of the long-haul seine (1.2 m) created some problems when sampling in shallow water. Organisms were trapped in folds of the netting as the net was being pulled past the post and escaped. Hundreds of organisms, especially the smaller finfish, probably escaped in this fashion at the shallow stations. All other gears proved adequate for marsh work in water depths ranging from 10 to 70 cm.

Mugil cephalus and *Elops saurus* easily leaped over the float lines of the seine; many were observed escaping from the net in this fashion. Both the 1.8-m otter trawl and the single push trawl had relatively small mouth openings, making avoidance of these gears easier. The push trawls required assembly in the field, and transportation of the net frames to the field was cumbersome, particularly for the double push trawl. It was difficult to set the push trawls at a sampling depth whereby the net frame would not become imbedded in the mud but would still sample the entire water column. All samples were retaken when net frames became imbedded in the bottom.

Number of Species

The most species were captured with the long-haul seine (39), while the single push trawl captured the fewest (25), and the other gears captured similar numbers of species (31-34) (Table 2). The long-haul seine also

TABLE 2

Number of species, mean number of species per sample, total numbers, mean number per sample and mean number/1000 m^2 captured with each gear.

	Long-haul Seine	Push Trawls		Otter Trawls	
		double	single	4.9-m	1.8-m
Number of species	39	34	25	32	31
Mean species per sample	10.0	8.9	6.6	8.5	7.3
Total number	45,491	48,449	20,560	7,273	12,710
Mean number per sample	1,421	1,514	642	250	397
Mean Number per 1000m^2	888	1,001	563	247	613

captured significantly more species per sample than the other gears (Table 3), averaging 10.0 species per sample, versus 8.9 for the double push trawl, 8.5 for the 4.9-m otter trawl, 7.3 for the 1.8-m otter trawl and 6.6 for the single push trawl (Table 2).

Number Per 1000 m^2 Sampled

A major source of variation within capture numbers was the differing area sampled by each gear. Maximum water depth during sampling was 65 cm,

TABLE 3

Results of Duncan's Multiple Range Test on number of species captured/sample and on log transformed catch of selected species/1000 m^2 for all gears. Gear catches are highest to lowest left to right, and those not underscored by the same line are significantly different.

Number of species/sample	**LHS**	**DPT**	SOT	LOT	**SPT**
Catch/1000m^2					
All taxa combined	LHS	DPT	SPT	SOT	LOT
Callinectes sapidus	**SOT**	LOT	LHS	DPT	SPT
Penaeus aztecus	LOT	SOT	DPT	LHS	SPT
Brevoortia patronus	LHS	DPT	SPT	LOT	SOT
Anchoa mitchilli	LHS	DPT	SPT	LOT	SOT
Micropogonias undulatus	LOT	LHS	**SOT**	SPT	DPT
Mugil cephalus	DPT	SPT	LHS	LOT	SOT
Cynoscion arenarius	**LHS**	LOT	DPT	SPT	SOT

* Gear abbreviations are: LHS long-haul seine, DPT double push trawl, SPT single push trawl, LOT 4.9-m otter trawl, SOT 1.8-m otter trawl.

mean water depth was 22 cm for the shallow stations and 46 cm at the deep stations. Except for the push trawls not sampling the bottom 3-8 cm, each gear fished the entire water column. Therefore, the surface area fished by each gear during a sampling run was determined and divided into the catch numbers for each sample taken to standardize data. The resulting figure was multiplied by 1000 to provide an estimate of the number of individuals captured per 1000 m^2 of surface area fished per sample. These catch per unit area values (Table 4) were then treated statistically as described above. Duncan's Multiple Range Test pinpointed significant differences among gears (Table 3).

The long-haul seine and double push trawl captured significantly more individuals overall than all the other gears (Table 3). The double push trawl had the highest catch/1000 m^2 (1,001) while the 4.9-m otter trawl had the lowest (247) (Table 4). The low catch of the 4.9-m trawl as compared to the other gears may be due to its inability to sample in extremely shallow water. Water levels were very low during the last two periods and only one sample was taken with the 4.9-m otter trawl at the shallow stations because the trawl boards would not stand up. Four samples were taken during this time at the shallow stations with each of the other gears. Also during this time, numbers of several cyprinodont forms (*Cyprinodon variegatus, Fundulus grandis, Poecilia latipinna*) were extremely numerous, elevating catch numbers of the other gears.

TABLE 4

Mean catch/1000 m^2 for all taxa combined and selected taxa by each gear.

SPECIES	GEAR				
	Long-haul Seine	Push Trawls		Otter Trawls	
		Double	Single	4.9-m	1.8-m
All	888.0	1001.0	563.0	247.0	612.0
Callinectes sapidus	4.2	3.3	2.0	8.0	16.4
Penaeus aztecus	7.0	32.8	10.3	43.1	39.2
Brevoortia patronus	513.2	370.0	128.3	64.9	68.6
Anchoa mitchilli	259.4	119.0	91.7	62.2	33.6
Micropogonias undulatus	17.5	1.3	2.5	24.8	10.7
Mugil cephalus	1.2	4.5	1.4	0.7	0.4
Cynoscion arenarius	1.1	0.1	0.0	0.4	0.0

The 1.8-m otter trawl captured significantly more *Callinectes sapidus*/1000 m^2 than all other gears (Table 3), capturing 16/1000 m^2, followed by the 4.9-m otter trawl with 8/1000 m^2 (Table 4). The greater catch of the 1.8-m otter trawl versus the larger, 4.9-m otter trawl may be due either to different trawling speeds or to mesh sizes. The 1.8-m trawl was pulled 0.45m/sec faster than the 4.9-m otter trawl, making net avoidance of the smaller otter trawl more difficult. During the first six periods, the 1.8-m otter trawl captured a greater percentage of *Callinectes sapidus* with carapace widths less than 20 mm (38% for the 1.8-m otter trawl versus 25% for the 4.9-m otter trawl). The push trawls probably captured fewer of these species because they are unable to catch organisms residing in or on the bottom sediments. The front bar of the push trawls was set to ride on the bottom and would tend to ride over any organisms directly on the bottom. Organisms would have to be a few centimeters off the bottom to be swept over the front bar and into the net. At the deeper stations we were unable to consistently set the push trawl so that the front of the frame would ride on the bottom sediments; organisms at those stations probably had to be several centimeters off the bottom for them to be captured. Although the long-haul seine sampled the bottom sediments, it took about five minutes from the time sampling was finished until the net could be lifted into the boat. Many *Callinectes sapidus* probably escaped during this time. It also moved relatively slowly, probably allowing many crabs to escape capture by burrowing into the bottom.

Penaeus aztecus results were similar to those for *Callinectes sapidus*. The otter trawls and the double push trawl captured significantly more *Penaeus aztecus* than the long-haul seine and single push trawl (Table 3). Catch/1000 m^2 was highest with the 4.9-m otter trawl, (43) followed closely by the 1.8-m otter trawl with 39. The long-haul seine probably captured few *Penaeus aztecus* for the same reasons cited above for *Callinectes sapidus*. The differ-

ence in catch between the push trawls is probably due to shrimp being able to avoid the mouth of the single push trawl (2.1 m wide), but not the wider mouth (4.2 m) of the double push trawl. Assuming 45% trawl efficiency using the 4.9-m otter trawl (Loesch *et al.* 1976), efficiency of the other gears for catching *Penaeus aztecus* is 40% (1.8-m otter trawl), 35% (double push trawl), 11% (single push trawl) and 8% (long-haul seine).

Brevoortia patronus was the most common finfish captured. There was no statistical difference in the number captured/1000 m^2 by the long-haul seine and the double push trawl (Table 3). The 1.8-m otter trawl captured the fewest/1000 m^2 but only slightly less than the 4.9-m otter trawl (Table 4). The high catch/1000 m^2 seen with the push trawls as compared to the otter trawls may be due to the ability of the push trawls to sample an area before it had been disturbed by the airboat. Fish were observed moving away from the airboat as it neared them, thus, the push trawls captured many gulf menhaden before they vacated an area, whereas the otter trawls captured only those that had not retreated from the area.

Results for *Anchoa mitchilli* were similar to those for *Brevoortia patronus*; the long-haul seine captured significantly greater numbers/1000 m^2 than all other gears except the double push trawl, and the otter trawls captured the fewest (Table 3). Differences between push and otter trawls are probably due to factors already described for *Brevoortia patronus*.

The 4.9-m otter trawl and the long-haul seine captured the greatest number of *Micropogonias undulatus*/1000 m^2 (Table 4), significantly more than the other gears (Table 3). Catch by the push trawls was least. The low push trawl catches are probably due to the inability of these gears to catch benthic organisms. Assuming 25% efficiency of the 4.9-m otter trawl (Loesch *et al.* 1976), efficiency of the other gears in capturing *Micropogonias undulatus* was 18% (long-haul) seine, 11% (1.8-m otter trawl), 2% (single push trawl) and 1% (double push trawl).

Few statistically significant differences were found among the sampling gears in the catch of *Mugil cephalus* (Table 3). Both push trawls captured the largest number/1000 m^2, and both otter trawls captured the least (Table 4). Differences in catch between push and otter trawls are probably due to factors discussed previously for *Brevoortia patronus*.

The long-haul seine captured the most *Cynoscion arenarius* (Table 3). This species, along with other larger and more mobile species (*Lepisosteus oculatus, Elops saurus, Pogonias cromis*) were taken in relatively small numbers, but most often were captured using the long-haul seine. While these species were able to avoid the openings of the push and otter trawls, they were less able to avoid being encircled by the seine.

SYNOPSIS

Each type of fishing gear used in this study varied widely in the type of species captured, number of species captured, number of individuals captured, and ease of use. Fisheries biologists should base their choice of

sampling equipment on the objectives of their study and their target species, not primarily on ease of use, equipment at hand, or expense.

Although difficult and time consuming to use, the long-haul seine captured the greatest number of species, the greatest number of species per sample, and greater numbers of individual organisms more often than any of the other sampling gears. Of those tested, it may be the preferred gear for the capture of anchovy, menhaden, most goby species, seatrout, ladyfish, drum, and gar. It is best used in an area slightly shallower than the depth of the net.

The push trawls were relatively easy to use, but were expensive and time-consuming to build and tended to capture large numbers of a few species of fish. The push trawls are best used when a researcher is interested in sampling both near-shore and open-water areas of a shallow, coastal marsh. They were highly maneuverable and their attachment to the front of a boat would allow them to be used close to a shoreline. A possible improvement for the push trawls would be to add a tickler chain several centimeters in advance of the mouth opening to force benthic organisms off the bottom. The double push trawl is more efficient than its smaller counterpart for most species and, of those tested, should be the gear of choice for all cyprin-odontiform species, silversides, grass shrimp and mullet. In water too deep to sample the entire water column it would be preferred to the otter trawl for the capture of surface swimming fishes.

Easiest and least expensive to use, the otter trawls appeared to have the lowest overall efficiency for capture of many species. However they were the most efficient gears for penaeid shrimp, spot, Atlantic croaker and blue crab.

In shallow water (< 1 m deep), a push-otter trawl (Rogers 1985) may be a good compromise between the push trawls and otter trawls used in our study. It would combine the positive aspects of push trawls (maneuverability, ability to catch organisms before disturbed by the airboat) with those of the otter trawls (ease of use, inexpensive, captures benthic organisms well) to provide one gear suitable for capture of all but the larger fish taxa.

LITERATURE CITED

BACKIEL, T. and R.L. WELCOMME. 1980. Guidelines for sampling fish in inland waters. *EIFAC Technical Paper No.* 33. 176 p.

CHABRECK, R.H. 1972. Vegetation, water and soil characteristics of the Louisiana coastal region. *Louisiana Agricultural Experiment Station Bulletin* No. 664. Baton Rouge, Louisiana.

HARTMAN, R.D. 1984. A study of the relative selectivity of six shallow, estuarine-marsh sampling gears and the distribution of fish and crustaceans in the Sabine National Wildlife Refuge, Louisiana. M.S. Thesis, Louisiana State University, Baton Rouge, LA. 119 p.

HERKE, W.H. 1969. A boat-mounted surface push-trawl for sampling juveniles in tidal marshes. *Progressive Fish-Culturist.* 31(3):177-179.

KJELSON, M.A. and D.R. COLBY. 1977. The evaluation and use of gear efficiencies in the estimation of estuarine fish abundance. In M. Wiley (ed.) *Estuarine Processes*, Volume 2, pp. 416-424. Academic Press. New York.

_____ and G.N. JOHNSON. 1974. Description and evaluation of a longhaul seine for sampling fish populations in offshore estuarine habitats. *Proceedings of the Annual Conference Southeastern Association of Game and Fish Commissioners.* 28:171-179.

_____ and _____. 1978. Catch efficiencies of a 6.1-meter otter trawl for es-

tuarine fish populations. *Transactions of the American Fisheries Society.* **107(2)**:246-254.

KUSHLAN, J.A. 1974. Quantitative sampling of fish populations in shallow, freshwater environments. *Transactions of the American Fisheries Society.* **103(2)**:348-352.

LOESCH, H., J. BISHOP, A. CROWE, R. KUCKYR and P. WAGNER. 1976. Technique for estimating trawl efficiency in catching brown shrimp (*Penaeus aztecus*), Atlantic croaker (*Micropogon undulatus*), and spot (*Leiostomus xanthurus*). *Gulf Research Report.* **5(2)**:29-33.

MACKETTS, D.J. 1973. Manual of methods for fisheries resource survey and appraisal. *FAO Fisheries Technical Papers* No. **124**. 40 p.

PERRY, W.G. 1978. Standing crops of fishes of an estuarine area in southwest Louisiana. *Proceedings of the Annual Conference of the Southeastern Association of the Fish and Wildlife Agencies.* **30**:71-81.

ROGERS, B.D. 1985. A small push-otter trawl for use in shallow marshes. *North American Journal of Fisheries Management.* **(3A)**:411-413.

SAS. 1985. *SAS Users Guide: Statistics.* 5th edition. SAS Institute, Inc. Cary, North Carolina. 956 p.

STEELE, R.G.D. and J.N. TORRIE. 1980. *Principles and procedures of statistics.* McGraw-Hill. New York. 630 p.

WATSON, J.W., Jr. 1976. Electric shrimp trawl catch efficiencies for *Penaeus duorarum* and *Penaeus aztecus. Transactions of the American Fisheries Society.* **105(1)**:135-148.

WEINSTEIN, M.P. and R.W. DAVIS. 1980. Collection efficiency of seine and rotenone samples from tidal creeks, Cape Fear River, North Carolina. *Estuaries.* **3(2)**:98-105.

Contributions in Marine Science. (1987) Vol. 30:27–37.

ORGANIC CARBON AND NITROGEN FLOW FROM MARINE CYANOBACTERIA TO SEMIAQUATIC INSECT FOOD WEBS

Warren M. Pulich, Jr.[1] and Richard S. Scalan

The University of Texas
Marine Science Institute
Port Aransas, Texas, 78373-1267

ABSTRACT

On coastal wind-tidal flats of South Texas, stable carbon isotopic composition of resident semiaquatic insects reflects the isotopic signature of cyanobacterial mats, the dominant primary producers. As evidenced by the abundance of insect populations, the transfer of marine cyanobacterial biomass to insect food webs is a major pathway of carbon flow in this intertidal environment. Three distinct plant nitrogen sources are delineated from the nitrogen isotope data set: blue-green algae, upland plants, and plants of a freshwater playa area; however, additional nitrogen measurements are necessary to demonstrate trophic relationships between insects.

INTRODUCTION

Wind-tidal flats in the Laguna Madre region of the northwestern Gulf of Mexico are a specialized intertidal habitat where large daily tidal fluctuations are absent and arid, windy climate exists (Sorenson and Conover 1962, Copeland 1966). Cyanobacteria (blue-green algae) of the genera *Lyngbya* and *Microcoleus* are the dominant benthic algae on such flats, forming extensive mats capable of significant primary productivity and nitrogen fixation (Pulich and Rabalais 1986). Despite the large amount of algal biomass produced, pathways of secondary production on these flats are poorly delineated. Due to the alternating cycles of tidal inundation and drying, the habitat is best described as semiaquatic with salt-tolerant insects comprising the dominant macrofauna present during non-flooded periods.

An abbreviated insect food web can be postulated for these flats during the predominant low tide exposure periods. Direct consumption of blue-green algal carbon and nitrogen can occur by the various herbivorous or phytosaprophagous groups found there (*e.g.* Collembola, Coleoptera and Diptera) (Daly, Doyen and Ehrlich 1978). In certain seasons, limnichid beetles and fly

[1] Resource Protection Division, Texas Parks and Wildlife Dept., 4200 Smith School Rd., Austin, TX 78744

larvae achieve standing stocks of thousands of individuals per square meter of algal mat (Pulich, unpublished results). These insect consumers in turn can provide food for the abundant predatory Hemipterans (*e.g.* shorebugs) and Coleopterans (tiger and carabid beetles) present (Daly *et al.* 1978). This proposed scheme represents a novel pathway of substantial, primary transfer of energy and material from marine algae to a semiaquatic food web.

While other marine ecosystems (*e.g.* salt marshes and seashore beaches) support minor associated insect food webs (Pfeiffer and Weigert 1981, Cheng 1976), the wind-tidal flats system appears unique in its domination by insect primary consumers.

Stable carbon and nitrogen isotopic compositions of the flora and insect fauna were investigated at a typical Padre Island, Texas wind-tidal flat. Previous isotope studies of marine ecosystems have traced carbon flow through salt marsh (Haines 1976, Hackney and Haines 1980), seagrass meadow (Thayer, Parker, La Croix and Fry 1978; Fry and Parker 1979; Fry, Lutes, Northam, Parker and Ogden 1982; Fry, Scalan and Parker 1983), mangrove community (Rodelli, Gearing, Gearing, Marshall and Sasekumar 1984), and phytoplankton-based food webs (Gearing, Gearing, Rudnick, Requejo and Hutchins 1984), but no isotope work has related to food web studies of habitats dominated by blue-green algae.

In each system, isotopic fractionation of carbon between consumers and their diets is 2 per mil (‰) at most, and generally much less (Fry and Sherr 1984). Thus the dominant plant species present in the ecosystem impart a characteristic isotopic signature to the organic carbon of consumer groups. The influence of seagrass or *Spartina* carbon is detectable as $\delta^{13}C$ values in the range of -10 to -15‰, while phytoplankton influence is represented by such values from -18 to -22‰, and mangrove carbon by values from -25 to -28‰.

Since the semiaquatic insects range from the flat margin (adjacent to C_3 and C_4 vegetation) to far out on the open flats, a large potential gradient exists between $\delta^{13}C$ of food sources. The diets of such insects could include C_3 plant carbon ($\delta^{13}C$ -22 to -29‰) or C_4 plant carbon ($\delta^{13}C$ -11 to -15‰) at the margin and algal mat carbon on the flats ($\delta^{13}C$ -12 to -14‰) (Behrens and Frishman 1971; Calder and Parker 1973; Fry, Jeng, Scalan and Parker 1978).

While carbon isotopic variations are related to the primary source of the element and vary by $\leq +2$‰ with the trophic level, nitrogen isotopic ratios depend not only upon the source of the nitrogen but are positively fractionated as much as $+3$ to $+5$‰ when passing from one trophic level to the next (Miyake and Wada 1967; Wada and Hattori 1976; Macko, Lee and Parker 1982; Rau 1982; Minigawa and Wada 1986; Wada, personal communication).

MATERIALS AND METHODS

The study site was located adjacent to the Upper Laguna Madre opposite Baffin Bay, Texas (Fig. 1). Collecting stations were established in three different plant habitats: "A" — on the open flats;

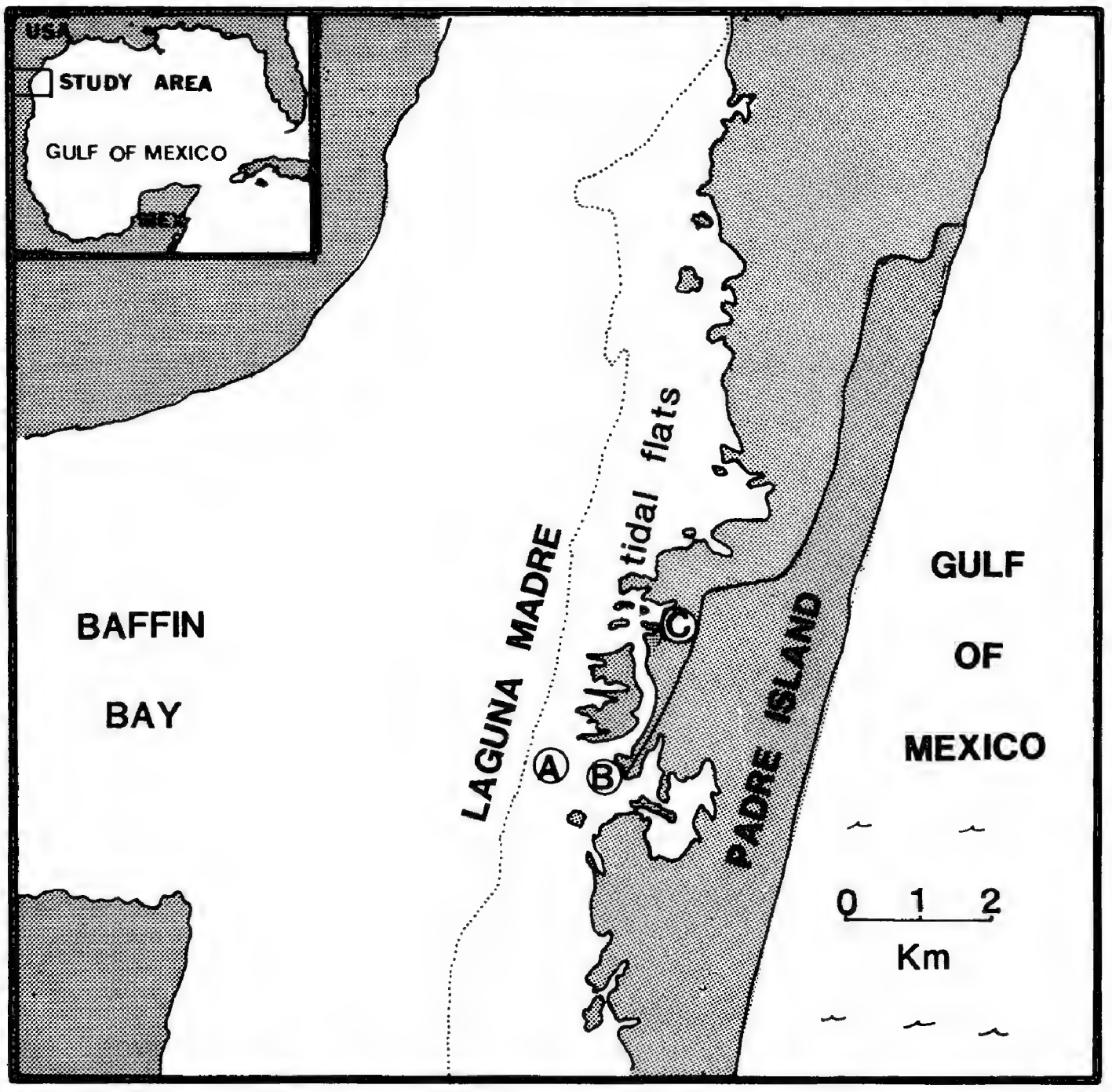


FIG. 1. Site map of Padre Island wind-tidal flat study area.

"B" — at the flat margin in the salt-tolerant vegetation; and, "C" — in a small, dried-up, freshwater playa about 1 km from the flat margin. Dominant insects were sampled at these stations during daylight hours five times in 1984 (5 June, 19 July, 5 September, 1 October, and 14 November) and on 22 August 1985. Specimens were captured with nets, picked by hand from surface algal mats, or dug from the sediments. Vascular plants at the two upland stations were collected at random and represent the most abundant local species.

The study primarily concentrated on resident, ground-dwelling insects (plus spiders) occurring at the three stations. Flying insects (*e.g.* flies) which breed and remain near the flats were also analyzed, since these appeared to be cons,umers of algal mats during their larval stage. A number of other flying insects (dragonflies, butterflies, *etc.*) were excluded, as they were considered transients to the flats.

All specimens were returned to the laboratory alive on the same day of collection and then were maintained frozen until they were oven dried at 90°C for 15 to 20 hours. Dried, whole insects or plant parts were cleaned by brushing if necessary and ground in a Wiley mill (40 mesh screen). Initially, all samples were treated with dilute HCl for thirty minutes to insure removal of carbonates. When carbonates were later determined to be absent in insects and vascular plants, only algal mat samples were subsequently acid-treated.

Carbon dioxide for $\delta^{13}C$ analysis was produced by a sealed-tube method adapted from Sofer (1980), using 5 to 10 mg dry weight of powdered sample when available. Following cryogenic purification of the carbon dioxide produced, isotopic measurements were made using an isotope ratio mass spectrometer (VG Micromass Ltd., Model 602E). Samples for nitrogen isotope measurements were prepared by a sealed-tube method similar to that of Macko (1981). Purified nitrogen gas was measured in a Model 6-60-RMS isotope ratio mass spectrometer (Nuclide Corporation).

The precision of isotopic measurements was determined by replicate analyses of samples and laboratory standards. For carbon analyses, the overall precision for biologic samples, including sample preparation and mass spectrometry, is ±0.17‰ for a 2 sigma range of pooled standard deviations from four measurements of samples run in triplicate. The standard deviation is ±0.061‰ for the four most recent periodic checks of standard preparation while the precision for the instrumentation alone is ±0.010‰. Precision for nitrogen isotopic analysis is somewhat less being approximately ±0.25‰ for overall sample preparation and measurement.

In most cases the analyses were performed on individual insects in an effort to establish the ranges of variation for each of several species. The only exceptions were for the minute limnichid beetles and collembola which required pooling of 20 to 50 individuals to give a sample of a size suitable for analysis.

TABLE 1

Carbon isotope values ($\delta^{13}C$) for selected biota of the Padre Island wind-tidal flat environment.

	A.	B.	C
Sample Type	Open Tidal Flats	Tidal Flat Margin	Freshwater Playa
PLANTS			
Cyanobacteria (mat)	-11.5±0.5(N=10)*		
Seagrass (detritus)		-11.8	
C_3 Plants			
Batis maritima		-22.4	
Bacopa monnieri			-24.4
Machaeranthera phyllocephala		-24.1	
Suaeda linearis		-24.4	
Eleocharis (sp.)			-24.6
Salicornia virginica		-25.7	
Borrichia frutescens		-26.0	
Sesuvium trianthemoides			-26.3
Salicornia bigelovii		-27.1	
Limonium nashii		-27.6	
Heliotropium curassivicum			-29.0
C_4 Plants			
Fimbristylis caroliniana			-10.6
Paspalum monostachyium		-11.5	-11.5
Schizachyrium scoparius		-11.7	-11.7
Panicum (sp.)		-12.4	
Spartina patens		-12.9	-12.9
Sporobolus virginicus		-13.3	-13.3
Flaveria oppositifolia		-13.7	
Monanthochlöe littoralis		-15.3	
INSECTS			
Coleoptera			
Carabidae			
Tachys pallidus		-12.9±1.0(N=3)	
Tachys (sp.)		-17.6±0.7(N=3)	
Diplochaetus lecontei	-14.3±1.3(N=7)	-15.5±2.0(N=2)	
Scarites subterraneus		-21.9	
Limnichidae	-14.0±0.6(N=2)		
Staphylinidae	-11.2	-17.5	
Chrysomelidae			-21.2

Cicindelidae			
Cicindela pamphila	-11.8±1.4(N=15)	-11.7±1.1(N=16)	
C. hamata	-19.3±2.4(N=17)	-17.5±2.5(N=22)	-17.0±2.5(N=13)
C. togata		-15.3±1.2(N=5)	-16.7±1.0(N=10)
Hemiptera			
Saldidae			
Pentacora sphacelata	-12.9±1.2(N=5)	-13.1±0.8(N=7)	-13.4
Lygaeidae		-23.4	
Pentatomidae		-22.9	
Collembola			
Poduridae		-14.4	
Orthoptera			
Gryllidae			
Nemobius (sp.)		-21.2	
Gryllus (sp.)		-20.5	
Diptera			
Bombyliidae			-20.2
Asilidae		-17.4±2.8(N=12)	-17.9±3.7(N=6)
Sphaeroceridae	-13.1	-13.3±0.3(N=2)	
(Sphaerocerid? pupae)	-11.4±0.0(N=2)		
Ephydridae	-12.9±0.4(N=2)		
(Coelopidae?)	-8.3		
Hymenoptera			
Formicidae			
(small)		-15.6	
(large)		-9.8	
SPIDERS			
Araneida			
Lycosidae	-13.1	-18.8±1.77(N=4)	

* Value represents mean ± one standard deviation for N individual samples. Single values are for a single sample.

RESULTS AND DISCUSSION

The carbon isotopic composition of dominant plants (Table 1) ranged from blue-green algal mat on the flats (at −11.2 to −12.6‰), to C_4 plants (mostly grasses at −12 to 14‰) and C_3 plants (−23 to −29‰) at the flat margin or surrounding the freshwater pond. Species surveys revealed the dominance of C_3 over C_4 plants at the flat margin and the fresh-water pond. At the flat margin, *Salicornia* spp., *Borrichia, Limonium, Batis* and *Machaeranthera* had much higher percent cover compared to grasses *e.g. Spartina* spp., *Sporobolus, Monanthochlöe* and *Paspalum.* At the freshwater playa, *Heliotropium, Bacopa, Sesuvium* and *Eliocharis* formed the entire vegetative community of the dried pond bed.

The most common macrofauna encountered on the exposed flats were the insects and spiders whose $\delta^{13}C$ values are listed in Table 1 (Column A). Phytosaprophagous species (*e.g.* limnichid beetles, various dipterans) yielded the most positive values (−8.3 to −14.0‰), while predatory types (carabid and rove beetles; shorebugs genus *Pentacora*) were slightly more negative (−11.2 to −14.3‰). The most common species of the predatory tiger beetles on the flats was *Cicindela pamphila*, which occurred during the summer and early fall months and appeared restricted to this environment

and the flat margin. It showed a narrow range of $\delta^{13}C$ values (-9.6 to -13.5‰, avg. -11.8‰). On the one occasion (22 August) when numbers of another species, *C. hamata*, were found on the flats, $\delta^{13}C$ values were substantially more negative (average -19.3‰, range -14.5 to -21.8‰). Thus, except for *C. hamata*, insect $\delta^{13}C$ values on the open flats were within ± 3‰ of the algal mat source of organic carbon (avg. $\delta^{13}C$ -11.5‰).

At the flat margin (Table 1, Column B), most of these insect species displayed a wider range of $\delta^{13}C$ values. Detritivores and microphytic grazers (*e.g.* Collembola, various dipterans, ants) showed more positive values (-13.3 to -15.6‰), while macrophytic herbivores (*e.g.* crickets and hemipterans) reflected the C_3 plant carbon (*ca.* -21 to -23‰). Among the predators, shorebugs (genus *Pentacora*) were the least negative (avg. -13.1‰) and two species of carabid beetles of the genus *Tachys* were distinguishable based on average $\delta^{13}C$ values (-12.9 *vs.* -17.6‰). Although three species of tiger beetles occurred in this habitat, only *C. hamata* indicated a wide selection of food sources $\delta^{13}C$ ranging from -10 to -21.8‰, avg. -17.5‰), typical of a generalist found in a variety of habitats (Fry *et al.* 1978). *C. pamphila* and *C. togata* appeared considerably less negative, averaging -11.9 and -15.3‰ respectively, with a maximum range from -11 to -17.2‰.

Except for the tiger beetles, *C. hamata* and *C. togata,* different species of insects occurred at the freshwater playa as compared to the tidal flats (Table 1, Column C). *C. pamphila* was not observed in this freshwater environment. *C. hamata* again showed the widest range of $\delta^{13}C$ (-13 to -20.5‰, avg. -17.0‰). *C. togata,* which occurred only during the warm spring and summer months, ranged from -15.8 to -19.5‰ (avg. -16.6‰). Common, potential food sources for tiger beetles in this environment (*viz.* chrysomelid beetles, bombyliid flies) exhibited $\delta^{13}C$ values close to -21‰. This station clearly demonstrated the maximum contribution of upland C_3 vegetation to the tissue carbon of these two species of tiger beetles.

Delta ^{13}C values for the predatory tiger beetle allow an assessment of possible feeding niches occupied by the three species (Fig. 2). A statistical evaluation of differences in population means of $\delta^{13}C$ of tiger beetles is given for ten cases of unequal populations in Table 3. The computed t-value, number of degrees of freedom, and probability of the means being equal are listed. There is a very great significance to the difference between *C. pamphila* and *C. hamata* $\delta^{13}C$ values on both the algal flat and at the flat margin, and between *C. togata* and *C. pamphila* at the margin. Lesser, but still significant differences are found for the $\delta^{13}C$ of populations of *C. hamata* between the algal flat and the flat margin and for *C. togata* between the flat margin and the fresh water playa. Other differences shown are of little or no significance.

The distribution of carbon isotope ratios was skewed toward negative values for all populations of *C. hamata* examined. In fact, $\delta^{13}C$ at the flat margin or on the open flats was more negative (avg. -17.5 and -19.3‰ respectively) than at the freshwater playa (avg. -17.0‰). In contrast to *C. hamata, C. pamphila* appeared to rely on a different food source whether at the flat margin or out on the open flat (range -10 to -13‰). Similarly, *C.*

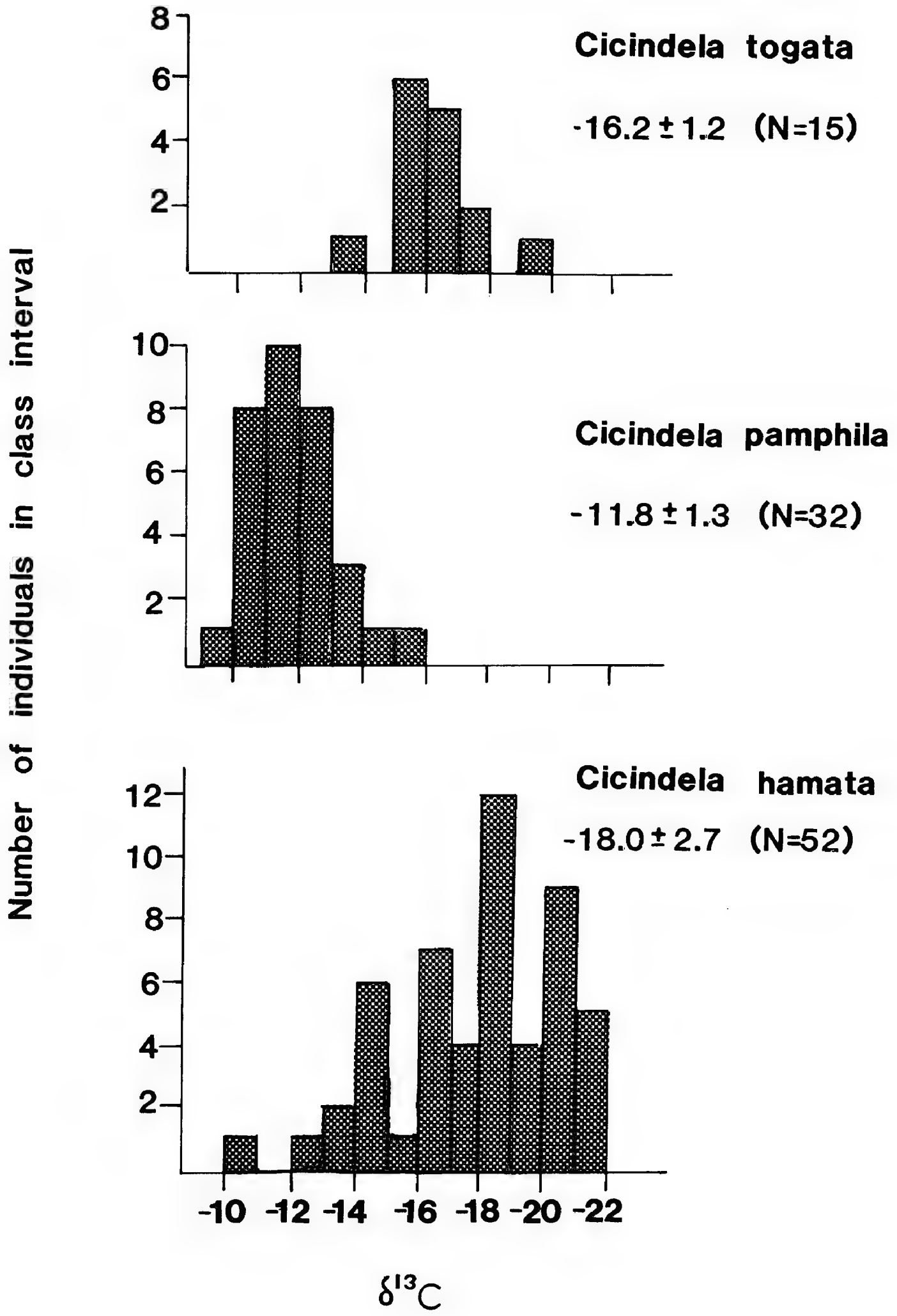


FIG. 2. Distribution of $\delta^{13}C$ values for three dominant species of tiger beetles found on or near the wind-tidal flat study area.

TABLE 2

Nitrogen isotope values ($\delta^{15}N$) for representative plants and selected animals of the Padre Island wind-tidal flat environment.

Sample Type	$\delta^{15}N$
PLANTS	
Blue-Green Algae mat layer	1.6 ± 0.5 (N =3)
Diatom-Green Algae layer	4.3
Halodule (detritus)	5.6
C_3 Plants (at flat margin)	
Salicornia virginica	7.4
S. bigelovii	6.8
Batis maritima	4.9
Borrichia frutescens	4.9
Limonium nashii	4.1
Suaeda linearis	4.1
C_3 Plants (at freshwater playa)	
Bacopa monnieri	-0.4
Heliotropium currassivicum	0.9
C_4 Grass	
Sporobolus virginicus	2.8
PRIMARY CONSUMERS	
Sphaerocerid fly pupal cases	0.8
PREDATORS	
Coleopterans	
Cicindela hamata	4.8 ± 1.3 (N =5)
C. togata	6.7 ± 0.9 (N =5)
C. pamphila	9.7 ± 2.3 (N =3)

togata used a narrow range of food at both the flat margin (−13 to −17‰) and the freshwater playa (range −16 to −19‰). These narrow ranges in food selection are typical of specialists restricted in feeding habits (Fry *et al.* 1978). Therefore, niche selection by *C. pamphila* and *C. togata* may be dependent on distinct food requirements satisfied only in the specific habitats they occupy.

The nitrogen isotopic composition of three distinct sources of plant nitrogen are given in Table 2. A +1.6‰ value for the blue-green algal mat represents the lowest trophic level for fixed nitrogen. This is significantly different from two other groups of plants growing in close proximity. Six species of C_3 plants growing at the margin of the algal flats had an average value of 5.4‰ and a single C_4 grass, *Sporobolus,* had a $\delta^{15}N$ value of 2.8‰. In the freshwater playa area the two dominant C_3 species of plants, *Bacopa* and *Heliotropium,* had nitrogen isotopic compositions much "lighter" than the blue-green algal mat (avg. 0.3‰). In this environment there may be several processes which fractionate the nitrogen isotopes to produce this effect. Possibly recycling of "upland" plant material could lead to the lower values by

TABLE 3

Tests of significance between two sample means of $\delta^{13}C$ of Cicindelids.

Variates (common attribute)	t	N	(p)
Cicindela pamphila-C.hamata (flat)	10.29	30	<<.001
C. pamphila-C. hamata (margin)	8.392	36	<<.001
C. pamphila-C. togata (margin)	5.868	19	<<.001
flat-playa (*C. hamata*)	2.480	28	~0.02
flat-margin (*C. hamata*)	2.164	37	~0.04
margin-playa (*C. togata*)	2.125	13	~0.05
C. hamata-C. togata (margin)	1.837	25	~0.09
margin-playa (*C. hamata*)	0.522	33	~0.61
C. hamata-C. togata (playa)	0.375	21	~0.71
flat-margin (*C. pamphila*)	0.163	29	~0.83

$$t = \frac{\tilde{x}_1 - \tilde{x}_2}{\left[\frac{\Sigma(x_{1i} - \tilde{x}_1)^2 + \Sigma(x_{2i} - \tilde{x}_2)^2}{N_1 + N_2 - 2} * \left[\frac{1}{N_1} + \frac{1}{N_2}\right]\right]^{\frac{1}{2}}}$$

$$N = N_1 + N_2 - 2$$

p = values interpolated from standard tables of t-test of significance.

incorporation of isotopically light ammonium or nitrate from rainwater (Wada, Imaizumi and Takai 1984). There also may be secondary sources of nitrogen, for example, atmospheric nitrogen fixed by a different primary producer having less fractionation than the blue-green algae of the open, saline flat environment (Macko, Entzeroth and Parker 1984). No algal mat material was evident in the playa area.

The only measurement in this study of nitrogen isotopic composition of a

primary consumer of the blue-green algal mat is represented by the pupal cases of the sphaerocerid flies. The $\delta^{15}N$ value of 0.8‰ is actually "lighter" than the algal mat material instead of "heavier" as predicted from previous studies. That is, there has been an apparent negative fractionation of the nitrogen isotopes in this instance. This fractionation may be complicated by the fact that the pupal cases consist almost solely of chitin, an end product of a specialized biochemical pathway. Since nitrogen isotope fractionation probably takes place in the biochemical pathways within the organism, this chitinous material may represent a "sink" for isotopically light nitrogen. Schimmelmann and DeNiro (1986) report isotopic heterogeneity for chitin of various arthropod sources including insects with the nitrogen being isotopically lighter for the chitin than for other animal portions. In the case of the cicindelids, the three tiger beetles were distinctly different in their nitrogen isotopic composition. *Cicindela hamata* was the lightest, *C. togata* was intermediate, and *C. pamphila* the most positive with values of 4.8, 6.7, and 9.7‰ respectively. Differences between these three predatory species may be attributed to the number of steps in their respective food webs from the initial plant sources to the grazers which are consumed by the tiger beetles. Thus, despite the fact that three distinct plant sources of nitrogen are recognizable at the Padre Island tidal flat, the flow of this nitrogen into the higher trophic levels is more difficult to follow compared to carbon. The precise food web of each animal species is, as yet, uncertain and is a good subject of further study, especially by nitrogen "stable isotope ecology."

ACKNOWLEDGMENTS

We wish to thank Dr. P. L. Parker of the University of Texas for his helpful discussions and Dr. Stan Wellso and his colleagues of the U. S. Department of Agriculture, Michigan State University for assistance in identification of some insect species. Funding was provided in part by the University of Texas and the Sid Richardson Foundation.

LITERATURE CITED

BEHRENS, E.W. and S.A. FRISHMAN. 1971. Stable carbon isotopes in blue-green algal mats. *Journal of Geology*. 79:94-100.

CALDER, J.A. and P.L. PARKER. 1973. Geochemical implications of induced changes in C_{13} fractionation by blue-green algae. *Geochimica et Cosmochimica Acta*. 37:133-140.

CHENG, L. ed. 1976. *Marine Insects*. North-Holland Publishers, Amsterdam. 581 pp.

COPELAND, B.J. 1966. Effects of decreased river flow on estuarine ecology. *Journal of Water Pollution Control Federation*. 38:1831-1839.

DALY, H.V., J.T. DOYEN and P.R. EHRLICH. 1978. *Introduction to Insect Biology and Diversity*. McGraw-Hill, N.Y. pp. 188-198.

FRY, B., W. JENG, R.S. SCALAN and P.L. PARKER. 1978. $\delta^{13}C$ food web analysis of a Texas sand dune community. *Geochimica et Cosmochimica Acta*. 42:1299-1302.

———, R. LUTES, M. NORTHAM, P.L. PARKER and J. OGDEN. 1982. A $^{13}C/^{12}C$ comparison of food webs in Caribbean seagrass meadows and coral reefs. *Aquatic Botany*. 14:389-398.

_____ and P.L. PARKER. 1979. Animal diet in Texas seagrass meadows: $\delta^{13}C$ evidence-for the importance of benthic plants. *Estuarine and Coastal Marine Science.* 8:499-509.

_____ and E.B. SHERR. 1984. $\delta^{13}C$ Measurements as indicators of carbon flow in marine and freshwater ecosystems. *Contributions in Marine Science.* 27:13-47.

_____, R.S. SCALAN and P.L. PARKER. 1983. $^{13}C/^{12}C$ ratios in marine food webs of the Torres Strait, Queensland. *Australian Journal of Marine and Freshwater Research.* 34:707-715.

GEARING, J.N., P.J. GEARING, D.T. RUDNICK, A.G. REQUEJO and M.J. HUTCHINS. 1984. Isotope variability of organic carbon in a phytoplankton-based, temperate estuary. *Geochimica et Cosmochimica Acta.* 48:1089-10-98.

HACKNEY, C.T. and E.B. HAINES. 1980. Stable carbon isotope composition of fauna and organic matter collected in a Mississippi estuary. *Estuarine and Coastal Marine Science.* 10:703-708.

HAINES, E.B. 1976. Stable carbon isotope ratios in the biota soils, and tidal water of a Georgia salt marsh. *Estuarine and Coastal Marine Science.* 4:609-616.

MACKO, S., L. ENTZEROTH and P.L. PARKER. 1984 Regional differences in stable nitrogen and carbon isotope ratios in the Gulf of Mexico. *Naturwissenschaften.* 27:S.374-375.

_____, W.L. LEE and P.L. PARKER. 1982. Nitrogen and carbon isotope fractionation by two species of marine amphipods: laboratory and field studies. *Journal of Experimental Marine Biology and Ecology.* 63:145-149.

MINIGAWA, M. and E. WADA. 1986. Nitrogen isotope ratios of red tide organisms in the East China Sea: A characterization of biological nitrogen fixation. *Marine Chemistry.* 19:245-259.

MIYAKE, Y. and E. WADA. 1967. The abundance ratios of $^{15}N/^{14}N$ in marine environments. *Records of Oceanographic Works in Japan.* 9:32-53.

PFEIFFER, W.J. and R.G. WEIGERT. 1981. Salt marsh consumers. pp. 87-112. In L.R. Pomeroy and R.G. Weigert (eds.) *The Ecology of a Salt Marsh.* Springer-Verlag, N.Y.

PULICH, W., JR. and S. RABALAIS. 1986. Primary production potential of blue-green algal mats on southern Texas tidal flats. *Southwestern Naturalist.* 31:39-47.

RAU, G.H. 1982. The relationship between trophic level and stable isotopes of carbon and nitrogen. pp 143-148.In W. Bascom (ed) Biennial Report for 1981-1982 of the Southern California Coastal Water Research Project. Long Beach, California.

RODELLI, M.R., J.N. GEARING, P.J. GEARING, N. MARSHALL and A. SASEKUMAR. 1984. Stable isotope ratio as a tracer of mangrove carbon in Malaysian ecosystems. *Oecologia.* 61:326-333.

SOFER, Z. 1980. Preparation of carbon dioxide for stable carbon isotope analysis of petroleum fractions. *Analytical Chemistry.* 52:1389-1391.

SORENSEN, L.O. and J.T. CONOVER. 1962. Algal mat communities of *Lyngbya confervoides* (Agardh) Gomont. *Publications Institute Marine Science University of Texas.* 8:61-74.

THAYER, G.W., P.L. PARKER, M.W. LA CROIX, and B. FRY. 1978. The stable carbon isotope ratio of some components of an eelgrass, *Zostera marina*, bed. *Occolgia* (Berl.) 35:1-12.

WADA, E., and A. HATTORI. 1976. Natural abundance of ^{15}N in particulate organic matter in the North Pacific Ocean. *Geochimica et Cosmochimica Acta.* 40:249-251.

_____, R. IMAIZUMI and Y. TAKAI. 1984. Natural abundance of ^{15}N in soil organic matter with special reference to paddy soils in Japan: biogeochemical implications on the nitrogen cycle. *Geochemical Journal.* 18:109-123.

Contributions in Marine Science. (1987) Vol. 30:39–47.

THE ROLE OF HURRICANES IN DETERMINING YEAR-CLASS STRENGTH OF RED DRUM

Gary C. Matlock

Texas Parks and Wildlife Department
4200 Smith School Road
Austin, Texas 78744

ABSTRACT

The hurricane season in Texas coincides with the red drum (*Sciaenops ocellatus*) spawning period. Hurricanes may impact year-class strength by increasing the numbers and/or survival of juvenile red drum recruited into bays. Bag seine collections during the period 1962-1975 in the Laguna Madre and Galveston Bay systems are used to examine recruitment after Hurricanes Beulah (1967) and Fern (1971). Trammel net collections during the same period in the lower Laguna Madre are used to examine year-class strength through age 3. Both hurricanes reduced bay salinities 20 to 25‰, and the number of juvenile red drum in the Laguna Madre increased. Year-class strength may have been increased through above average transport of larvae to nutrient-rich bays and higher survival rates in intermediate salinities (15-25‰) caused by hurricanes.

INTRODUCTION

The red drum (*Sciaenops ocellatus*) is an estuarine-dependent sciaenid that ranges from Tuxpan, Mexico in the Gulf of Mexico to Massachusetts in the Atlantic Ocean (Matlock 1984). Adults spawn in the nearshore oceanic waters from August through January with a peak in September or October. Larvae (2-11 mm) are transported through passes into estuarine nurseries where they remain for 3 to 5 years before returning to the ocean or gulf. Economically important estuarine fisheries exist throughout most of its range. The strength of these fisheries depends in part on the transport of eggs and larvae to suitable nursery areas.

The hurricane season coincides with the spawning peak for red drum. Strong tidal surges and heavy rains in estuaries usually result. So, hurricanes may play a major role in producing strong year classes of red drum. Recent work on Pacific mackerel (*Scomber japonicus*) and other marine fishes indicates that recruitment variability is closely linked to large-scale climactic events (Sinclair, Tremblay and Bernal 1985; Winters, Wheeler and Dalley 1986). Between 1962 and 1974, Hurricanes Cindy, Beulah and Fern moved across the Texas coast during the peak red drum spawning period (Sep-Oct) (Henry, Driscoll amd McCormack 1975). Hurricane Cindy made landfall

north of Galveston, Texas, on 17 September 1963. Hurricane Beulah moved inland between Brownsville, Texas and the mouth of the Rio Grande River on 20 September 1967, and affected the coast from Matagorda Bay to the lower Laguna Madre with 25 to 76 cm of rain and heavy flooding in 4 days. Hurricane Fern moved inland near Matagorda on 10 September 1971 and moved south toward Laredo. Almost 12 and 9 cm of rain fell on Corpus Christi and Brownsville, respectively, in 24 hours (NOAA 1971a, 1971b) causing some of the worst flooding since Hurricane Beulah (Kingston 1985). Hurricane Edith moved parallel to the Texas coast in the Gulf of Mexico during 11-30 September 1971.

Breuer (1968) reported a "bumper crop" of red drum produced in 1967 as a result of Hurricane Beulah. However, he presented little supporting evidence and did not address possible causative mechanisms. This study presents additional data that indicate that strong year classes of red drum occur after some hurricanes. The possible role of salinity reductions caused by hurricanes in increasing red drum survival is examined.

MATERIALS AND METHODS

Fish caught in bag seines in the Laguna Madre (affected area) and Galveston Bay (unaffected area) were used to determine abundance of juveniles during the period 1962-1975. However, data from Galveston Bay were collected only during 1962 through 1969. Multifilament bag seines were 18.3 m long and 1.8 m deep with a 1.8-m square bag in the center and 9.5-mm stretched mesh webbing. Seines were pulled along shore in a standard fashion at three to ten stations monthly where seiners thought they would catch juvenile (age 0, 20 to 100 mm total length) red drum and spotted seatrout (Breuer 1968, Matlock 1984). The net was extended from shore, pulled about 30 m with one end on shore, and the end in the water was pulled to shore while the end on shore remained stationary. Mean annual catch (no./hectare) in each bay system was calculated by pooling data for each year from all seine hauls during the period January-June; fish could escape the gear in other months. Standard errors of the pooled monthly means were calculated because data from individual seine hauls no longer exist. Plots of these means (± 1 SE) for the Laguna Madre were visually compared to those for Galveston Bay.

Sub-adult relative abundance in the lower Laguna Madre during fall (Oct-Nov) 1961 through spring (April-May) 1975 was determined using multifilament trammel nets. Nets were 366 m long, 1.2 m deep with 7.6-cm and 22.8-cm stretched mesh in the inside and outside walls, respectively (Matlock 1984). They were used during the day each fall and spring 2-3 times at 12 sites where netters thought they would catch red drum and spotted seatrout. No collections were made in spring 1964 or fall 1967. Each net was set in the shape of a rectangle (100 x 200 m) with the shore as one side (200 m). The enclosed area was struck by driving the boat through the area and slapping the water with oars (Dailey, Matlock amd Hegen 1986). Each red drum was counted, and the total length (TL) was measured to the nearest 5 mm. The mean number of red drum caught per set (no./set) in each season each year and associated standard errors were calculated using a ratio estimator (Cochran 1977). Ages were assigned to each fish caught during spring 1968-1975 based on its TL and the age-TL key of Matlock (1984), and the mean no./set was calculated for each age class in the catch. Mean monthly salinities in the Laguna Madre and Galveston Bay systems for the period January 1962 through December 1975 were obtained from Martinez (1965, 1966, 1967, 1968, 1970, 1971, 1972, 1973, 1974, 1975), Hawley (1963, 1964, 1965), Johnson (1964, 1965), More (1965) and Osburn (1963). Plots of these data were visually inspected to determine the relationship between hurricanes and salinity and year-class strength of red drum.

RESULTS

Hurricane Cindy (1963) had no apparent effect on salinity or red drum year class strength. Salinities in the Laguna Madre before and after this hurricane remained at 40 to 50‰ (Fig. 1). Mean bag seine catches after Cindy were

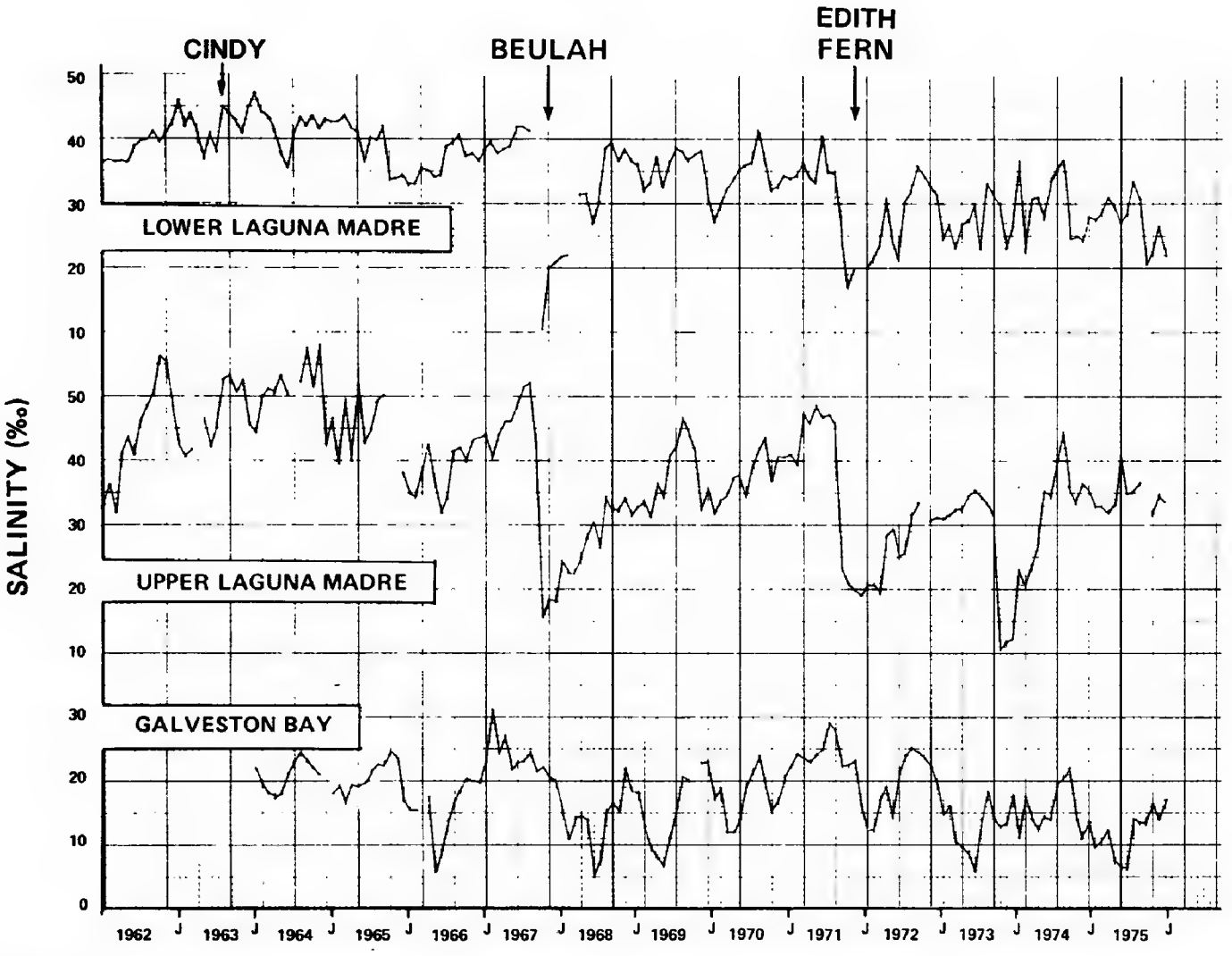


FIG. 1. Mean monthly surface salinity (‰) in the Laguna Madre and Galveston Bay systems during 1962 through 1975. Arrows indicate years of hurricanes affecting Texas coast.

similar to those before (Fig. 2). No salinity data were available for Galveston Bay before January 1964, but mean bag seine catches fluctuated without pattern immediately before and after the hurricane (Fig. 2).

Hurricane Beulah greatly reduced salinities, and the number and/or survival of red drum recruited to the Laguna Madre increased in fall 1967. These fish were first caught in bag seines in 1968, and catches in the upper and lower Laguna Madre were higher in 1968 than in any other year (Fig. 2). Catches in the unaffected Galveston Bay system in 1968 were similar to those in other years. Catches in the lower Laguna Madre were generally increasing before Hurricane Beulah (Fig. 2) as salinities were decreasing from about 45‰ (Fig. 1). Catches in the upper Laguna Madre and Galveston Bay during the pre-Beulah period were generally stable or varied without pattern (Fig. 2). Salinities in the upper Laguna Madre before Hurricane Beulah generally

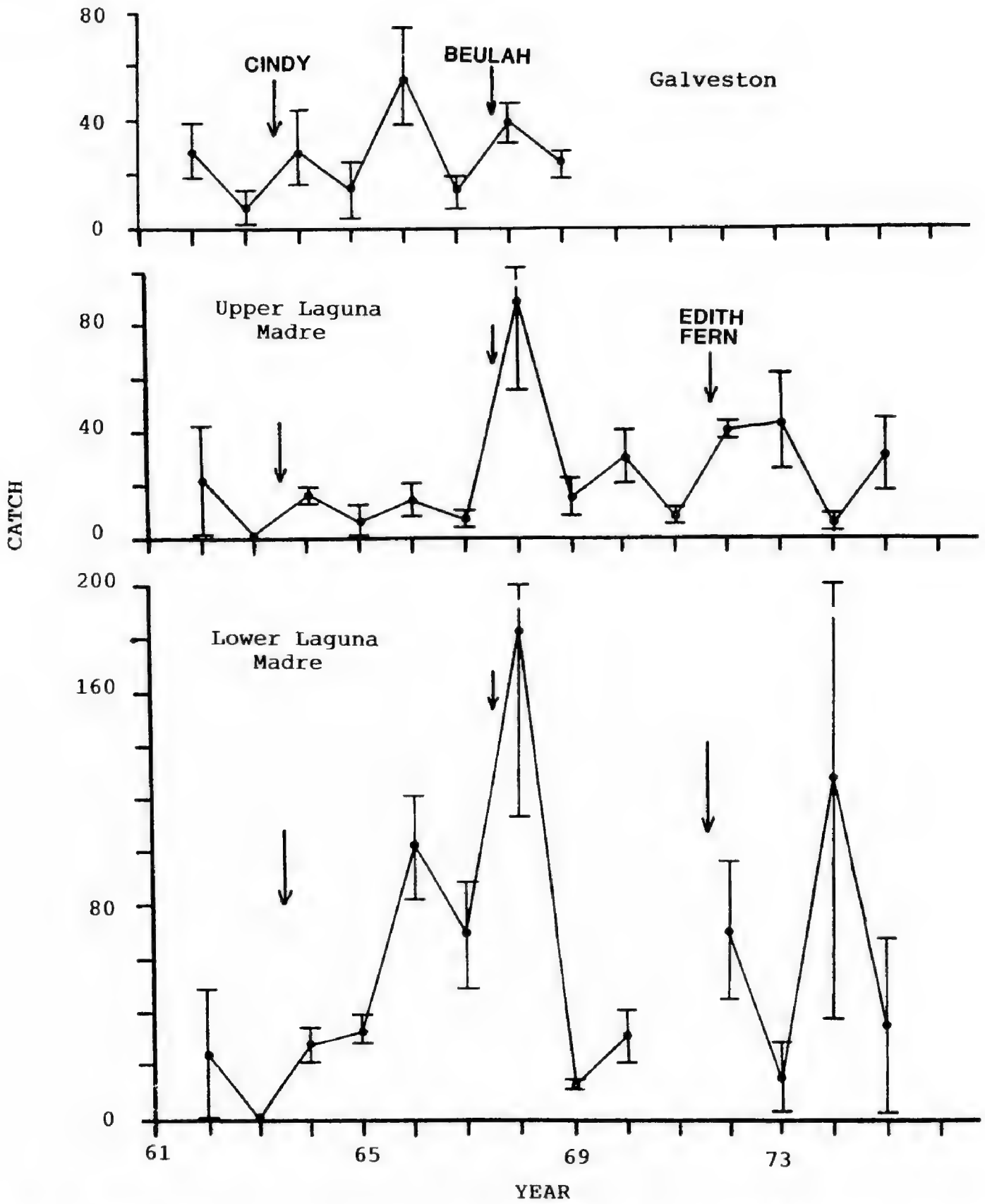


FIG. 2. Mean juvenile (age 0) red drum catch (no./ha) in bag seines during the period January-June each year in the Laguna Madre and Galveston Bay systems. Arrows indicate years of Hurricanes Cindy (1963), Beulah (1967), and Fern and Edith (1971).

increased to about 60‰, decreased to about 30‰ and then increased to about 50‰ (Fig. 1). Salinities in Galveston Bay fluctuated without pattern between 15 and 25‰ (Fig. 2).

The strong 1967 year class was evident in trammel nets in the lower Laguna Madre in fall 1968 (Fig. 3) and for 3 years thereafter (Fig. 4).

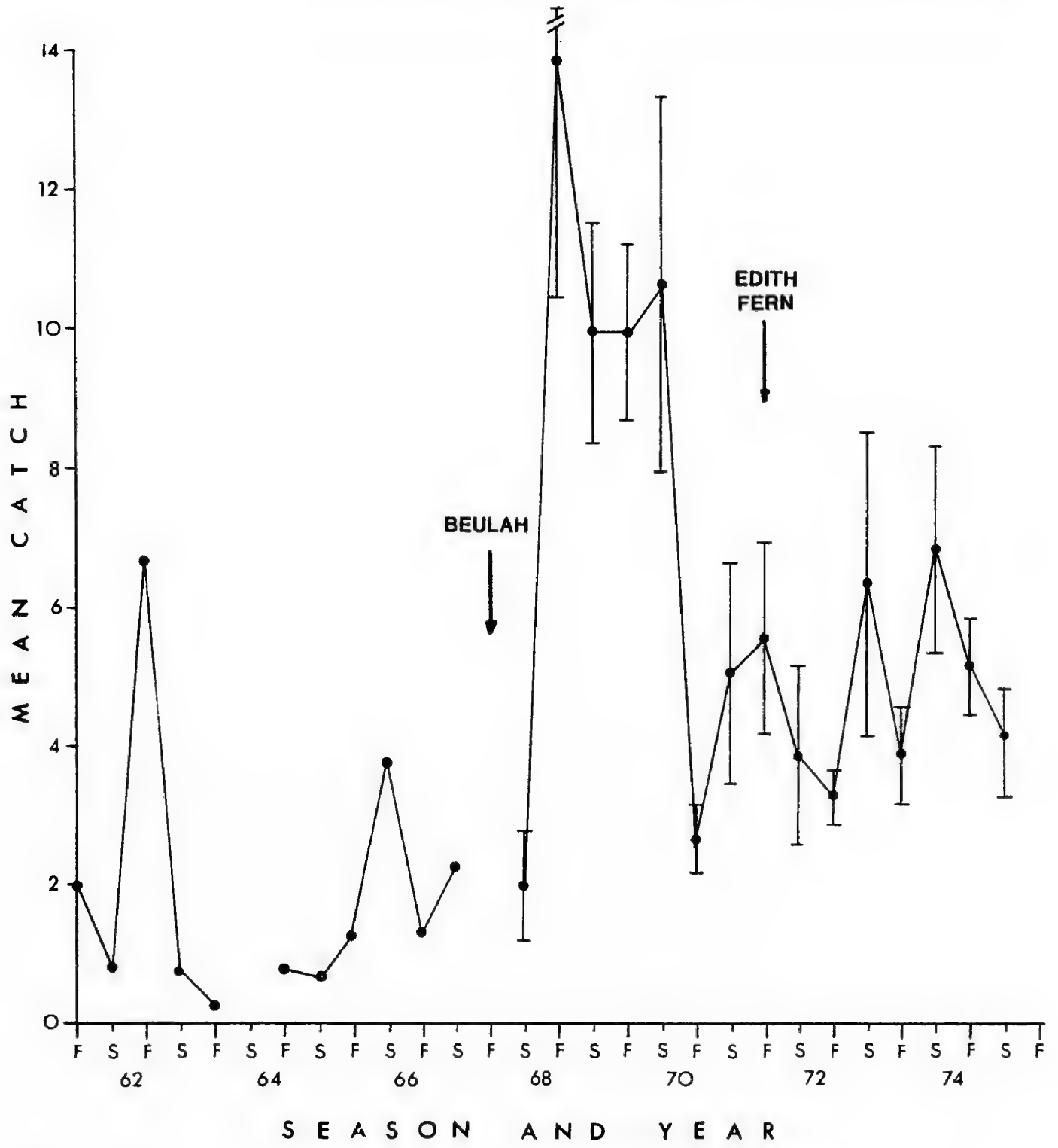


FIG. 3. Mean catch (no./set) of sub-adult red drum in trammel nets in the lower Laguna Madre each fall (F) and spring (S) during the period 1961-1974. Arrows indicate years of hurricanes affecting Texas coast.

Bag seine catches in the Laguna Madre also increased in 1972. Mean monthly salinities dropped 20 to 25‰ in fall (Aug-Oct) 1971 with the passage of Hurricane Fern. However, no bag seine collections were made in the Galveston Bay system. The strong 1971 year class in the lower Laguna Madre was evident in trammel nets in fall 1972 and spring 1973 as age I fish, in fall 1973 as age II, and fall 1974 as age IV fish (Fig. 4). However, the total fish caught in trammel nets after Hurricane Fern did not increase until spring 1973 (Fig. 3).

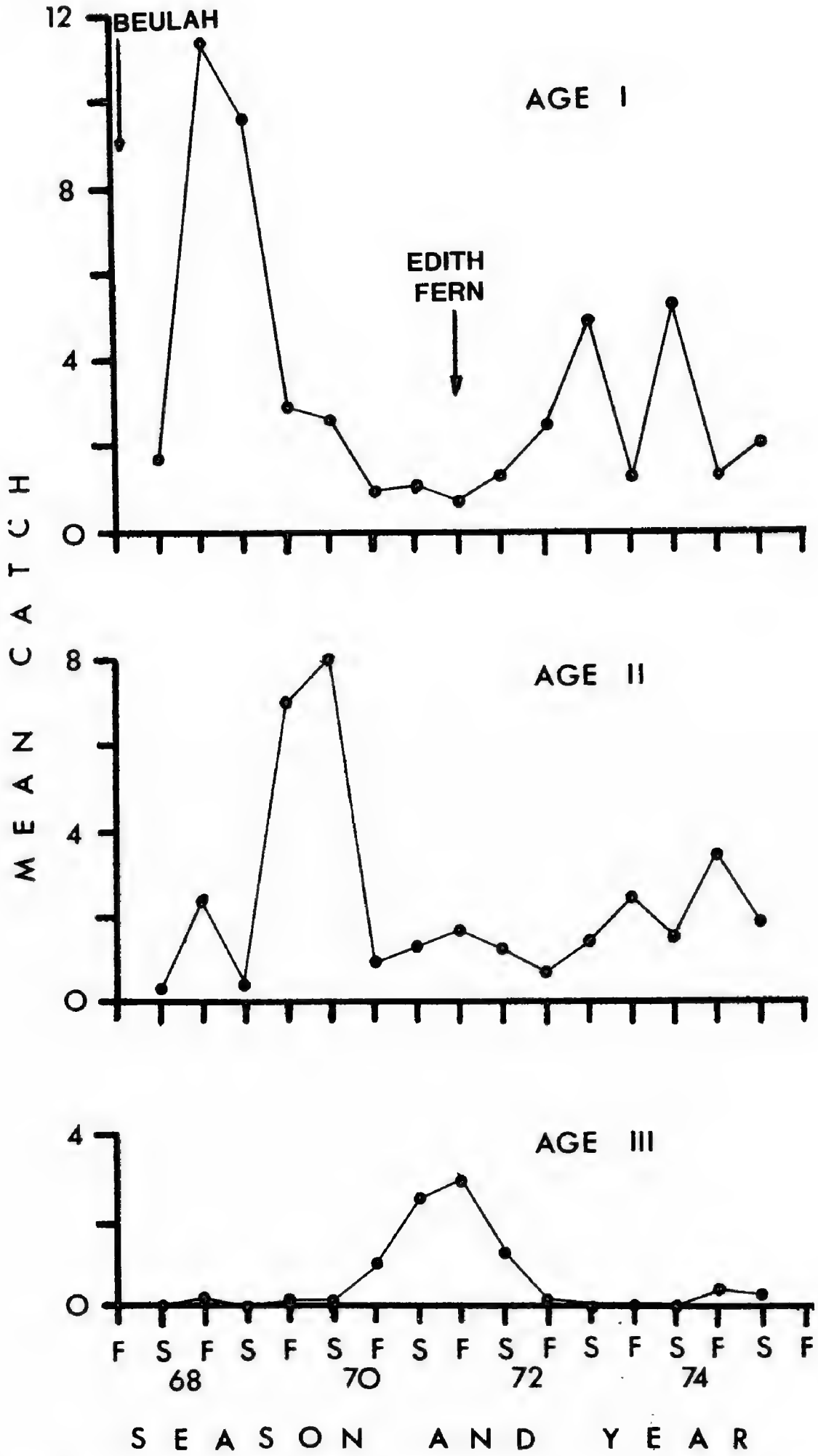


FIG. 4. Mean catch (no./set) of each age class of red drum in trammel nets in fall (F: Oct-Nov) and spring (S: Apr-May) in the lower Laguna Madre during the period 1968-1975. Age III probably also includes age IV fish. Arrows indicate years of hurricanes affecting Texas coast.

DISCUSSION

Hurricanes can probably increase red drum year-class strength (recruitment) through a series of events affecting several life history stages. This multistage development of year-class success resembles that proposed by Sette (1950). A greater number of larvae can be transported to low salinity, nutrient-rich estuarine nurseries during and after hurricanes than normally occurs. Pelagic eggs and larvae are passively transported from gulf spawning sites through barrier island passes (Matlock 1984, Norcross and Shaw 1984, Shaw, Wiseman, Turner, Rouse and Condrey 1985). Hurricanes can increase the volume of water subsequently entering estuaries by temporarily creating new passes and by storm surges through existing passes. For example, before Hurricane Beulah there were no continuously open bay-gulf passes into the upper Laguna Madre, but at least three passes were opened for several months after Beulah (Martinez 1967). Tides were almost 2 m above normal along the entire coast in late September 1967 (Martinez 1967).

Survival of these newly recruited larvae during the "critical period" (Hjort 1913) is probably enhanced by an abundant food supply, especially rotifers and zooplankton, created by enhanced productivity. Episodic climactic events that produce freshwater input stimulate primary productivity by providing a new source of nutrients (Flint 1985). Hurricanes Beulah and Fern produced heavy rains and major flooding in the Laguna Madre. But, Beulah had a much greater effect than Fern in the lower Laguna Madre (Henry *et al.* 1975). This may explain why recruitment to bag seines was greater after Beulah than Fern. It may also explain why age I red drum were not recruited to trammel nets until 18 months after birth during Fern as opposed to 12 months after Beulah. Growth after Fern may have been slower than after Beulah. However, no data are available to examine this possibility.

Salinity reduction in estuaries caused by hurricanes can also have negative effects. Survival of 24-hour red drum larvae was about 80% at 30‰ and 65% at 15‰ in the laboratory (Holt, Godbout amd Arnold 1981). However, as red drum grow, tolerance to low salinity (10‰) increases (Crocker, Arnold Deboer and Holt 1981). Salinities in the Laguna Madre after Hurricanes Beulah and Fern may not have declined sufficiently to reduce larval survival. Salinities were averaging 40 to 50‰ before each hurricane and dropped to 10 to 20‰ two months later.

If hurricanes affect year class strength by increasing recruitment to suitable estuarine environments, then stocking hatchery-reared fish directly into estuaries may increase red drum abundance during low recruitment years. However, many biotic and abiotic factors, including food availability, predator types and densities, habitat amount and quality, and environmental conditions will play a role in determining stocking success. For example, if salinity rapidly declines below 10‰ shortly after stocking, survival will probably be low. Matlock, Kemp and Heffernan (1986) reported there was no survival of stocked fish in August 1980 after Hurricane Allen dropped salinities in St. Charles Bay, Texas to 0‰. This salinity reduction may have

directly affected survival through increased osmotic stress (Holt *et al.* 1981) or indirectly by reducing the primary food supply of juvenile red drum (Colura, Matlock and Maciorowski 1988). Additional research is needed to quantify the relationships between red drum recruitment and these factors.

LITERATURE CITED

BREUER, J. P. 1968. Analysis of populations of sports and commercial fin-fish in the coastal bays of Texas. p. 45-66. In Coastal Fisheries Project Reports, 1968. Texas Parks and Wildlife Department, 134 p.

COCHRAN, W. G. 1977. *Sampling techniques.* John Wiley and Sons, New York, 428 p.

COLURA, R. L., G. C. MATLOCK, AND A. F. MACIOROWSKI. 1988. Zooplankton abundance in unstocked mariculture ponds at three salinities. *Progressive Fish-Culturist* (in press).

CROCKER, P. A., C. R. ARNOLD, J. A. DEBOER, AND J. D. HOLT. 1981. Preliminary evaluation of survival and growth of juvenile red drum (*Sciaenops ocellata*) in fresh and salt water. *Journal of the World Mariculture Society* **12(1)**:122-134.

DAILEY, J., G. C. MATLOCK, AND H. E. HEGEN. 1986. Catchability coefficients for coastal fishes caught in 366-meter and 732-meter long trammel nets struck with noise and rotenone. *Estuaries.* **9(48)**:348-355.

FLINT, R. W. 1985. Long-term estuarine variability and associated biological response. *Estuaries.* 8:158-169.

HAWLEY, W. 1963. Hydrographic and meteorological study of the upper Laguna Madre. p. 1-4. In Marine Fisheries Project Reports, September 1961-December 1962. Texas Game and Fish Commission.

_____. 1964. Hydrographic and meteorological study of the upper Laguna Madre. p. 473-478. In Coastal Fisheries Project Reports, 1963. Texas Parks and Wildlife Department, 590 p.

_____. 1965. Hydrographic and meteorological study of the upper Laguna Madre. p. 499-504. In Coastal Fisheries Project Reports, 1964. Texas Parks and Wildlife Department, 635 p.

HENRY, W. K., D. M. DRISCOLL, AND J. P. MCCORMACK. 1975. Hurricanes on the Texas coast, description and climatology. Texas A&M University, College of Geosciences, Center for Applied Geosciences, TAMU-SG-75-501, 27 p.

HJORT, J. 1913. Fluctuations in the great fisheries of northern Europe. *Rapports et Proces-Verbaux des Reunions. Conseil Permanent International pour l'Exploration de la Mer.* **19:1**-228.

HOLT, J., R. GODBOUT, AND C. R. ARNOLD. 1981. Effects of temperature and salinity on egg hatching and larval survival of red drum, *Sciaenops ocellata. Fishery Bulletin.* **79(3)**:569-573.

JOHNSON, R. B. 1964. Hydrographic and meteorological study of the lower Laguna Madre. p. 479-485. In Coastal Fisheries Project Reports, 1963. Texas Parks and Wildlife Department. 590 p.

_____. 1965. Hydrographic and meteorological study of the lower Laguna Madre. p. 505-512. In Coastal Fisheries Project Reports, 1964. Texas Parks and Wildlife Department. 635 p.

KINGSTON, M. 1985. *Texas Almanac, 1986-1987.* Dallas Morning News, A. H. Belo Corporation, Communications Center, Dallas, Texas, 768 p.

MARTINEZ, R. 1965. Coastal hydrographic and meteorological study. p. 169-212. In Coastal Fisheries Project Reports, 1965. Texas Parks and Wildlife Department, 255 p.

_____. 1966. Coastal hydrographic and meteorological study. p. 105-146. In Coastal Fisheries Project Reports, 1966. Texas Parks and Wildlife Department, 168 p.

_____. 1967. Coastal hydrographic and meteorological study. p. 77-112. In Coastal Fisheries Project Reports, 1967. Texas Parks and Wildlife Department, 112 p.

_____. 1968. Coastal hydrographic and meteorological study. p. 95-134. In Coastal Fisheries Project Reports, 1968. Texas Parks and Wildlife Department, 134 p.

_____. 1970. Coastal hydrographic and meteorological study, 1969-1970. p. 227-344. In Coastal Fisheries Project Reports, 1969-1970. Texas Parks and Wildlife Department, 344 p.

_____. 1971. Coastal hydrographic and meteorological study. p. 135-190. In Coastal Fisheries Project Reports, 1971. Texas Parks and Wildlife Department, 227 p.

_____. 1972. Coastal hydrographic and meteorological study. p. 146-197. In Coastal Fisheries Project Reports, 1972. Texas Parks and Wildlife Department, 197 p.

_____. 1973. Coastal hydrographic and meteorological study, 1973. p. 111-172. In Coastal Fisheries Project Reports, 1973. Texas Parks and Wildlife Department, 202 p.

_____. 1974. Coastal hydrographic and meteorological study, 1974. p. 61-108. In Coastal Fisheries Project Reports, 1974. Texas Parks and Wildlife Department, 130 p.

_____. 1975. Coastal hydrographic and meteorological study. p. 100-157. In Coastal Fisheries Project Reports, 1975. Texas Parks and Wildlife Department, 196 p.

MATLOCK, G. C. 1984. A basis for the development of a management plan for red drum in Texas. Ph.D. Dissertation, Texas A&M University, College Station, Texas 272 p.

_____, R. J. KEMP, JR., and T. L. HEFFERNAN. 1986. Stocking as a management tool for a red drum fishery, a preliminary evaluation. Texas Parks and Wildlife Department, Coastal Fisheries Branch, Management Data Series, No. 75. 27 p.

MORE, W. R. 1965. Hydrographic and meteorological study of the Galveston Bay system. p. 413-424. In Coastal Fisheries Project Reports, 1964. Texas Parks and Wildlife Department, 635 p.

NOAA. 1971a. Local climatological data, annual summary with comparative data, Corpus Christi, Texas, 1971. U.S. Department of Commerce, N.O.A.A., Environmental Data Service, 4 pages.

NOAA. 1971b. Local climatological data, annual summary with comparative data, Brownsville, Texas 1971. U.S. Department of Commerce, N.O.A.A., Environmental Data Service, 4 pages.

NORCROSS, B. L., AND R. F. SHAW. 1984. Oceanic and estuarine transport of fish eggs and larvae: a review. *Transactions of the American Fisheries Society*. 113:153-165.

OSBURN, K. W. 1963. Hydrographic and meteorological study of the lower Laguna Madre. p. 1-8. In Marine Fisheries Project Reports, September 1961-December 1962. Texas Game and Fish Commission.

SETTE, 0. E. 1950. Structure of a research program to determine how fishing affects the resources. *U. S. Fish and Wildlife Service, Special Scientific Report, Fisheries*. 15:1-30.

SHAW, R. F., W. J. WISEMAN, JR., R. E. TURNER, L. J. ROUSE, JR., and R. E. CONDREY. 1985. - Transport of larval gulf menhaden *Brevoortia patronus* in continental shelf waters of western Louisiana: a hypothesis. *Transactions of the American Fisheries Society*. 114:452-460.

SINCLAIR, M., M. J. TREMBLAY, and P. BERNAL. 1985. El Nino events and variability in a Pacific mackerel (*Scomber japonicus*) survival index: Support for Hjort's second hypothesis. *Canadian Journal of Fisheries and Aquatic Scientists*. 42:602-608.

WINTERS, G. H., J. P. WHEELER, AND E. L. DALLEY. 1986. Survival of a herring stock subjected to a catastrophic event and fluctuating environmental conditions. *Journal du Conseil*. 43:26-42.

Contributions in Marine Science. (1987) Vol. 30:49–61.

THE VERTICAL DISTRIBUTION AND FEEDING ECOLOGY OF *EUCHAETA MARINA* IN THE EASTERN GULF OF MEXICO

P.G. Shuert and T.L. Hopkins

Department of Marine Science
University of South Florida
St. Petersburg, Florida 33701

ABSTRACT

Euchaeta marina is an abundant carnivorous copepod in the epipelagic zone of temperate to tropical latitudes. During summer months in the eastern Gulf of Mexico most of the population occurred above 100 meters throughout the diel period, however diel vertical migration was apparent. The daytime center of the total population was near 50 meters. At dusk the population ascended, the center occurring at 20-30 meters by night fall. The centers of adult and copepodid V stages showed a midnight descent from near the surface to 40-60 meters followed by a pre-dawn ascent to around 10-15 meters. Copepodid stages IV and smaller gave no evidence of a midnight descent and remained centered at 30 meters throughout the night. Cyclic feeding was apparent with feeding rates in adult females being higher at night than during the day. The diet of adult females consisted of small crustaceans less than 1 mm body length. Adult males do not feed. The daily impact of predation by *Euchaeta marina* on metazoan zooplankton was estimated at less than 1% of the total available resources.

INTRODUCTION

The copepod *Euchaeta marina* is an important predator in the epipelagic zooplankton community from temperate to tropical latitudes (VerVoort 1963). In the subtropical northeastern Atlantic numerical abundance was estimated at 0.54% of the copepod population (Roe 1972). Our data show it to be 3 to 8% of the total copepod population by numbers in the upper 1000 meters of the eastern Gulf of Mexico (Hopkins 1982; Hopkins, Bennett and Shuert 1979) making it one of the dominant copepod species and the most abundant member of the genus. Aspects of trophic ecology have been studied for a number of *Euchaeta* species. Diet composition has been investigated for *Euchaeta media, E. hebes, E. acuta, E. concinna, E. norvegica, E. scotti* and *E. timidula* (Geinrikh 1958, Wickstead 1962, Mullin 1966, Harding 1974) and experimental work on prey selectivity has been done on *E. elongata* (Yen 1982) and *E. norvegica* (Bamstedt and Holt 1978). No information is available on feeding chronology for any member of this genus, and the reported information on the natural diet of this family of copepods has been based on

analysis of relatively few specimens.

Data for this study were obtained during the summer months at 27°N, 86°W in the eastern central Gulf of Mexico between 1975 and 1982. This station, while essentially in oligotrophic boundary waters, has many tropical-subtropical gyre characteristics (Vinogradov 1970, McGowan 1974, Longhurst 1976, Hopkins 1982). The location has been well studied as to species composition, diel distribution and standing crop of both zooplankton and micronekton (Hopkins 1982, Morris and Hopkins 1983, Hopkins and Lancraft 1984) and investigations have been made on the trophodynamics of a number of the zooplankton and micronekton species (Hopkins and Baird 1977, Baird and Hopkins 1981, Heffernan and Hopkins 1981, Hopkins and Baird 1981, Hopkins and Baird 1985a,b, Bennett 1986). This paper adds to this growing body of information by reporting on the trophic ecology of *Euchaeta marina*. Information will be presented on its vertical distribution, diet composition and feeding chronology. A consideration of the impact of this abundant predator on its available resources will also be discussed.

METHODS

Plankton samples used for this study were taken on two summer cruises in 1975 and 1976 on the R/V COLUMBUS ISELIN, and two summer cruises in 1980 and 1982 on the R/V BELLOWS. R/V COLUMBUS ISELIN samples (designated CI) were taken with 162 μm mesh collapsible square-mouth plankton nets, either 0.19 m^2 or 0.44 m^2 in the mouth area, which were mounted in the mouth of a closing Tucker Trawl (see Hopkins and Baird 1975; Hopkins, Baird and Milliken 1973). Depth was controlled with a conducting cable-depth transducer system. Tows were horizontal and depth variation was limited to ± 5 meters. A detailed explanation of these samples is presented in Hopkins (1982).

R/V BELLOWS samples (designated FS) were collected using 202 μm mesh, circular-mouth opening/closing plankton nets, either 0.28 m^2 or 0.44 m^2 in mouth area. Depth was monitored using wire angle and a meter wheel, and was recorded with a time-depth recorder. In most cases multiple nets were fished simultaneously at several depth horizons.

Trawling speed was two knots and tow duration ranged from 13 to 136 minutes (Table 1). The volume of water sampled was estimated with digital flowmeters mounted in the mouth of each net, these recording only when nets were open.

TABLE 1

Collection Data

CRUISE	DATE	# SAMPLES USED	RANGE OF TOW DURATION IN MINUTES AND AVERAGE IN PARENTHESES
R/V COLUMBUS ISELIN	June 1975	46	45-93 (57)
R/V COLUMBUS ISELIN	June 1976	14	42-136 (63)
R/V BELLOWS	June 1980	26	13-34 (34)
R/V BELLOWS	July 1982	24	18-72 (34)

Euchaeta marina were preserved, sorted and counted in both FS and CI collections using either an entire sample or an aliquot. Individuals from FS samples were also counted, measured and then sex and developmental stage determined. Total body length, from the tip of the rostrum to the end of the caudal rami, was measured to the nearest 0.1 mm.

Total number of *E. marina* from FS and CI samples were grouped into twelve 2-hour time intervals to reveal the diel distribution pattern of the total population. Additionally, FS data were re-grouped into eight 3-hour time intervals to show individual diel vertical patterns for each sex and for the later copepodite stages. Mean depth of the population, the depth above which 50% of the individuals resided, was calculated for each time interval. This depth was defined as the population center.

Forty-six FS samples were used to investigate feeding chronology in adult females, copepodid IV and younger stages. Histological preparations were made on 10 undamaged individuals from each sample and each developmental group when sufficiently abundant using standard histological techniques. Consecutive 7 μm thick sections were cut and mounted on slides for staining. The slides were stained with hematoxylin and eosin.

Longitudinal sections through the gut were examined for the amount of food in the fore- and mid-gut areas combined and in the hind-gut area. An average of 10 sections were examined for each copepod, enabling a composite three-dimensional picture of gut fullness to be developed. Based on the composite picture, an arbitrary scale of 0 to 4 was used to indicate the degree of fullness where 0 = empty, 1 = 25% full, 2 = 50% full, 3 = 75% full, and 4 = 100% full. Thus, category 1 would represent the lowest and category 4 the highest level of feeding.

Diet composition was analyzed by examining all sections of 40 adult females with full guts (category 4) and 10 adult males.

RESULTS

Vertical Distribution and Population Structure

The vertical distribution data of the four cruises were combined for Figures 1 and 2. The combination was justified because analysis of several years of data revealed little interannual change in vertical structure of dominant species. The vertical distribution patterns in Figs. 1 and 2A indicate that *Euchaeta marina* maintained a population center near 50 meters during the day. There was a net upward movement at dusk with a new center at 20 to 30 meters by 2000 hrs. Subsequently there was a period of sinking of the population center near midnight (0000-0200 hrs.) which was followed by a second apparent migration toward the surface before dawn. Shortly after dawn the population center returned to the daytime depth of 50 meters where it remained until dusk. This diel pattern was apparent in each of the data sets (*i.e.*, both the FS and CI series) used in preparing Figs. 1 and 2A.

Although the mean depth of the population (Figs. 2A-E) is considered a less reliable indicator of synchronous movements in a population (Pearre 1979), the period of sinking from the surface described above is apparent in Fig. 1 (0000-0200), where 10 samples taken above 30 meters show few individuals present compared with the 8 samples taken below this depth which show at least 4 times the number of individuals.

Based on FS samples, adults of both sexes and copepodid stage V individuals (Figs. 2B-E) showed little variation in vertical distribution from that described above for the total population. However, copepodid IV and smaller stages (Fig. 2F) maintained a nighttime population center at 30-40 meters and did not

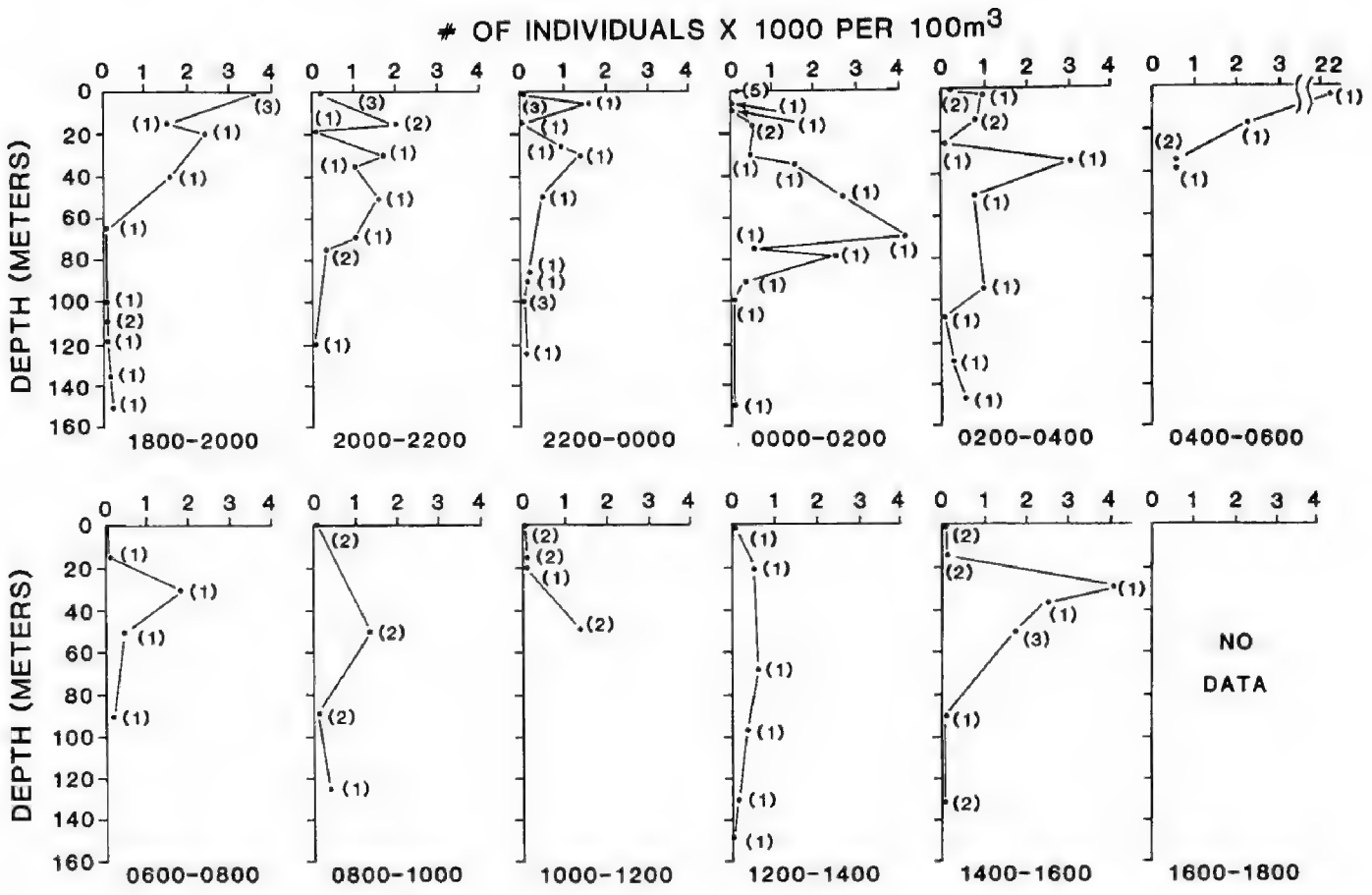


FIG. 1. Total number of *Euchaeta marina* per 100 m *versus* depth (meters), grouped in 2-hour intervals. Number in parenthesis are the number of samples taken at that depth. No data were taken between 1600 and 1800 hrs. Both CI and FS samples were used.

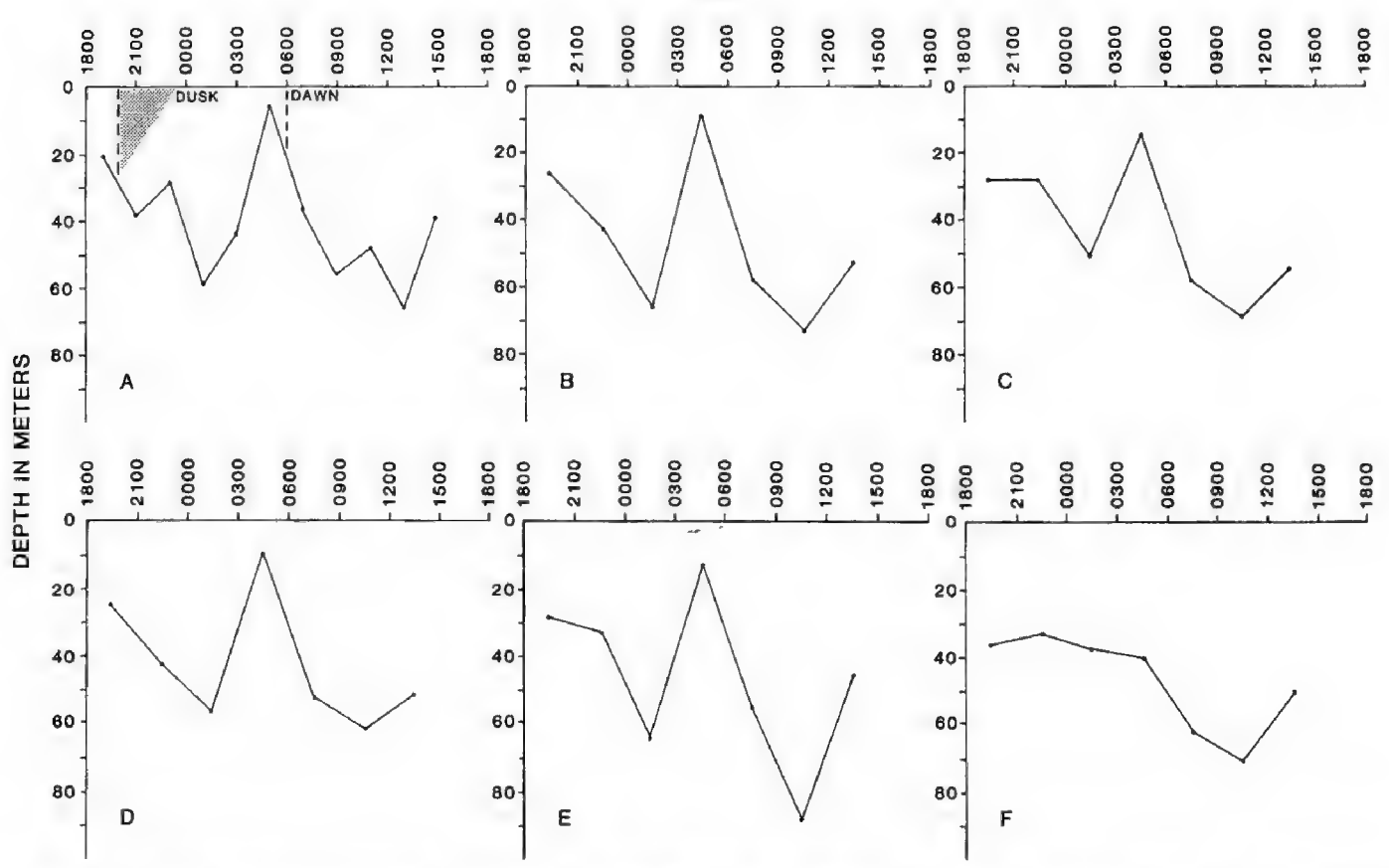


FIG. 2. Depth of population means over 24 hours: (A) total number of individuals; (B) adult males; (C) adult females; (D) gravid females; (E) copepodid stage V males and females; (F) copepodid stages IV and earlier, both males and females. A includes FS and CI samples combined at 2 hour intervals. B-F includes FS samples only, at 3 hour intervals.

show the "midnight sinking" pattern. Shortly after dawn and throughout the day, the distribution of copepodid IV and younger stages coincided with that of the remainder of the population.

The combined percentage of immature and mature females (65%) in the population was nearly twice that of males (35%) based on FS samples (Table 2). The percentages of adults of both sexes combined (35%), copepodid stage V (30%) and remaining earlier stages (35%) in these collections were roughly equal. The percentage of the last category is probably artificially low because of escapement losses of the smaller *Euchaeta* stages through the plankton net meshes. Gravid females, identified as those with attached egg sacs, were 6% of the population or approximately one-third of the adult female numbers. The actual abundance of gravid females was probably under-estimated since some of the egg sacs may have been dislodged during sample processing. Egg sacs contained a mean of 10 blue eggs (range 5 to 13) which averaged 0.28 mm in diameter.

Feeding

All fullness data were grouped into hourly intervals to determine feeding chronology. The percentage of individuals that showed categories 1 through 4 was plotted against time to represent the chronology of individuals that fed at least at a minimum level. A second plot was made of the percentage of individuals that showed a category of ≥ 2. This was taken to represent individuals that had greater success in feeding. Plotted with this, was the percentage of individuals with at least a category 2 or higher hindgut fullness. The two plots were overlaid to follow passage of food through the gut.

TABLE 2

Numerical distribution of sexes and copepodid stages of *Euchaeta marina*. Data are from FS samples only (see Methods).

Class	Average %	Range
Males	35	6-57
Females	65	43-94
Adults	35	0-75
Adult males	(8)	(0-24)
Adult females (non-gravid)	(20)	(0-25)
Gravid females	(6)	(0-26)
Stage V	30	2-86
Stage V males	(19)	(0-57)
Stage V females	(11)	(0-33)
Stage IV and smaller	35	0-98

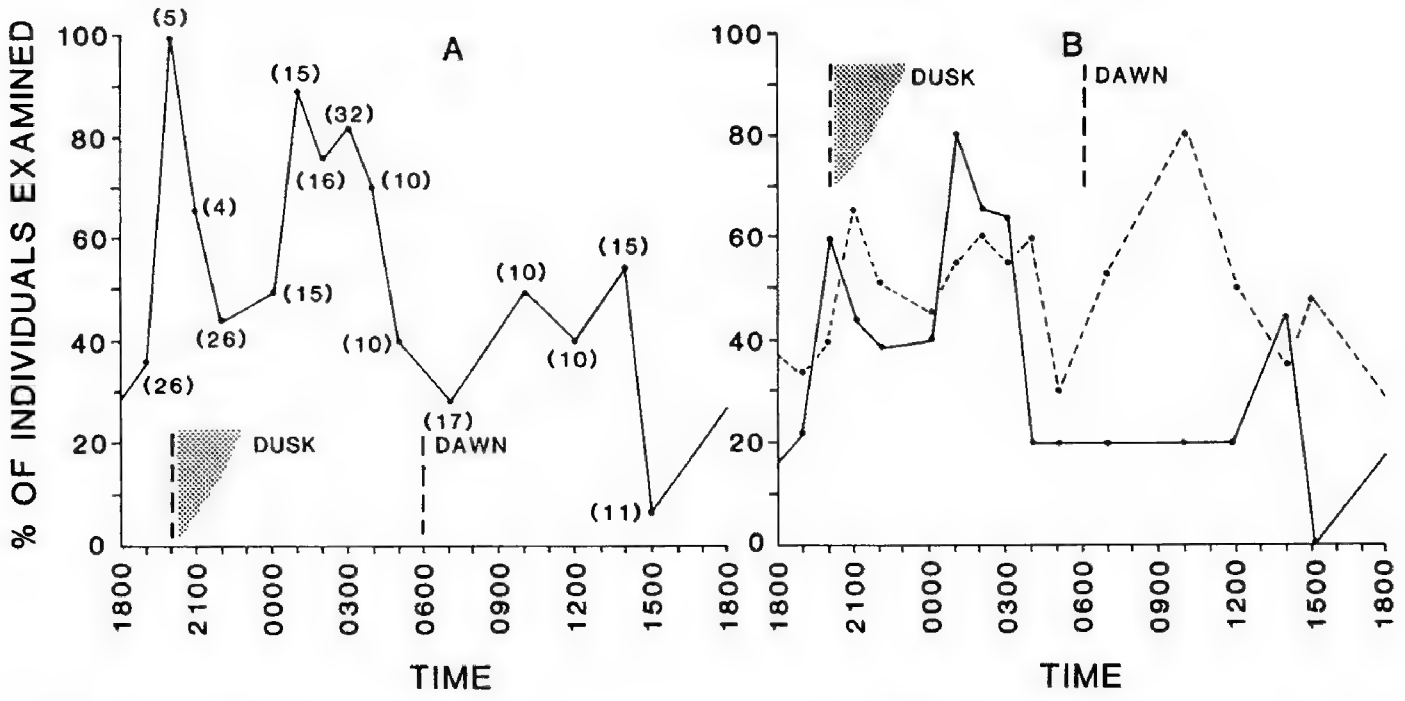


FIG. 3. Feeding chronology of adult females (A) Percent of individuals examined with 25% or greater of fore- and mid-gut fullness. Number of individuals examined for each time interval is in parenthesis. (B) Percent of individuals examined with 50% or greater of fore- and mid-gut fullness (solid line) and 50% or greater of hind-gut filled (dashed line). Number of individuals examined is the same as in (A). Dawn and dusk are indicated.

Results of gut fullness studies (Fig. 3A) indicated that adult females fed to some extent throughout the diel cycle but with a higher percentage of individuals showing evidence of feeding at night. Figure 3B, which presents data for only the more "successful" feeders (gut fullness categories 2-4), reveals that a rapid increase in fore- and mid-gut fullness occurred by early evening (2000 hrs). This was followed by a three-hour period of decline. Then gut fullness increased and was highest at 0100 hrs, with 80% of the individuals examined showing category 2-4 gut fullness. During the morning (0400-1200 hrs), incidences of category 2-4 gut fullness in the population decreased to an average of 20% of the individuals examined. This was followed by an increase to a 45% incidence at 1400 hrs. In mid-afternoon (1500 hrs) guts were least full, with none of the individuals examined containing food (Fig. 3B). The percentage of hind-guts with 50% or greater fullness tracked combined fore- and mid-gut fullness (Fig. 3B), though displaced one hour later. We looked for depth related trends in feeding activity of adult females from different depth horizons but found none.

Figure 4 shows the results of feeding chronology analysis for night samples (1800-0600 hrs) of combined copepodid IV and younger stages of males and females. Generally, feeding levels for these groups were low throughout this period, although some minor peak periods were evident. Based on those individuals with 50% or greater gut fullness, feeding intensity increased at 2200 hrs, this being followed by a decline by 0100 hrs to near zero level. Our data show a second apparent increase in feeding intensity between 0400-0500 hrs.

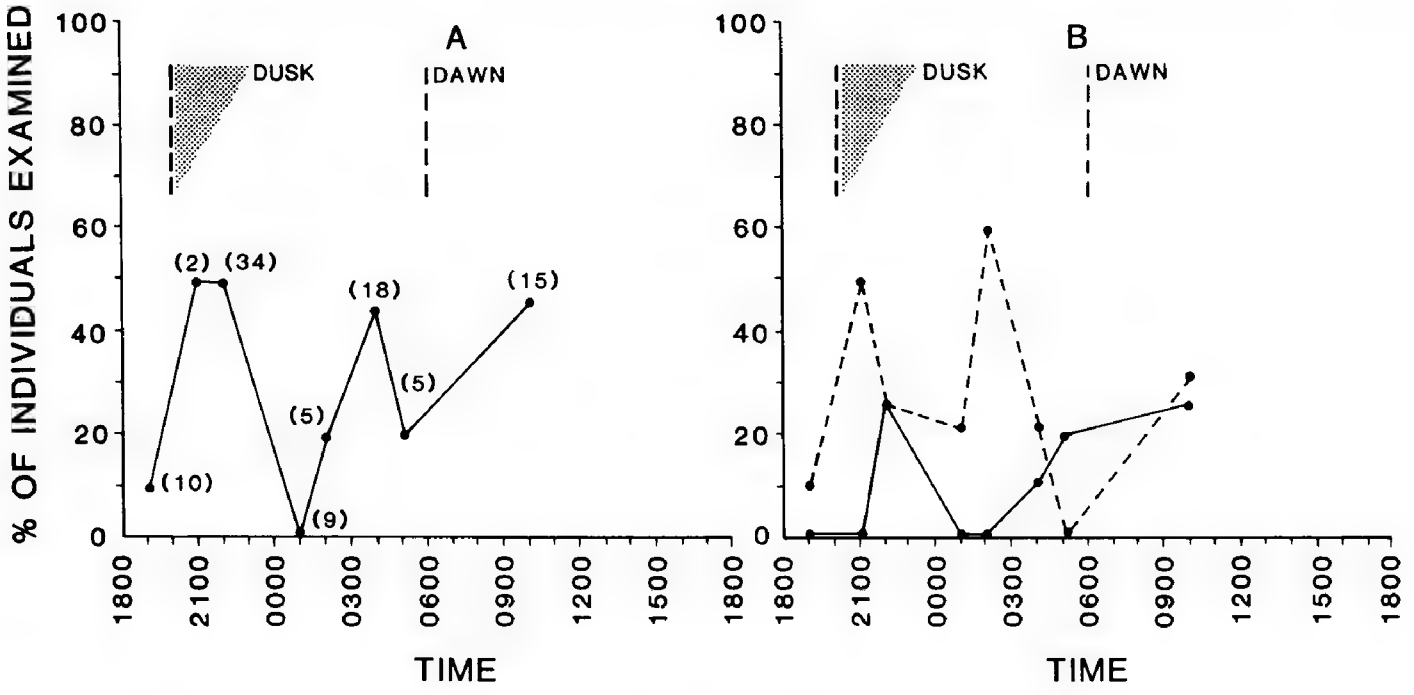


FIG. 4. Feeding chronology of copepodid stage IV and earlier stages of both males and females combined. (A) Percentage of individuals examined with 25% or greater fore- or mid-gut fullness. Number of individuals examined is in parenthesis. (B) Percentage of individuals examined with 50% or greater fore- and mid-gut fullness (solid line), and the percentage of individuals examined with 50% or greater of hind-gut fullness (dashed line). The number of individuals examined is the same as in (A). Dawn and dusk are indicated.

The diet composition study based on fore-and mid-gut contents indicated that adult female *E. marina* ingest small crustaceans, primarily copepods. Identifiable copepods were mostly small harpacticoids and cyclopoids (Table 3). Some fragments of early copepodid stages of calanoids were found as well. Among the recognizable food were fragments of species of *Oncaea, Microsetella,* and *Centropages*.

Adult males appeared not to feed. Histological examination revealed thin, thread-like guts which contained no food. Feeding appendages, for example the mandible and maxillipeds, were also noticeably reduced in sized compared to those of females and younger male stages.

DISCUSSION

Vertical Distribution and Feeding Chronology

Other studies have shown the vertical depth range of *E. marina* can be exte,nsive, in excess of 2 kilometers in the Caribbean (Owre and Foyo 1967, Roe 1972) and in the Atlantic (Leavitt 1938). However the species is essentially epipelagic in these areas with as much as 96% of the population occurring in the upper 100 meters. Data for the eastern Gulf of Mexico are similar, indicating that the vertical range of *E. marina* is at least 1 kilometer but with most of the population occurring in the upper 100 meters (Hopkins 1982, and present study). Using night samples and integrating over depth there were an average of 1355 individuals under a square meter of sea surface in the upper 100 meters at 27°N, 86°W.

TABLE 3

Stomach contents of 40 adult female *Euchaeta marina*

Copepod No.	Stomach Contents
1	copepod mandible and 2nd maxilliped
2	crustacean fragment
3	*Oncea* fragments; copepod fragments
4	copepod fragments
5	copepod fragments
6	crustacean fragments
7	*Microsetella* fragments
8	*Pleuromamma* pigment organ; copepod fragments
9	harpacticoid-like thoracic segments
10	crustacean fragments; copepod 2nd maxilliped
11	*Centropages*-like fragments
12	crustacean spines; fragments
13	2 copepod mandibles; *Corycaeus*-like fragments
14	copepod fragments; piece of feeding appendage
15	copepod fragments
16	amphipod-like gnathopod
17	harpacticoid-like spines
18	crustacean fragments
19	copepod fragments
20	*Oncaea* periopod segment
21	*Oncaea*-like periopod segment;crustacean spines
22	crustacean spines
23	copepod fragments
24	mandible; crustacean spines
25	copepod periopod segment
26	copepod-like fragments
27	copepod-like feeding appendage
28	crustacean spines and fragments
29	copepod fragments
30	*Oncaea*-like periopod segment; crustacean fragments
31	crustacean spines
32	crustacean fragments; spines
33	copepod fragments; crustacean spines
34	crustacean fragments
35	harpacticoid-like periopod segment
36	copepod fragments
37	copepod-like fragments
38	crustacean spines
39	copepod-like fragments
40	copepod mandible; crustacean fragments

Diel vertical patterns of *Euchaeta marina* vary regionally. Roehr and Moore (1965) located the population center at 154 meters during the day and 104

meters at night in the Florida Straits. Roe (1972) on the other hand indicated a possible reverse migration in which the population descended from 40 meters during the day to 50 meters at night. The present data show a daytime center near 50 meters with an ascent to near 30 meters occurring after dusk (1800 hrs). A period of sinking occurs around midnight which is followed by a second ascent to near the surface just prior to dawn. *E. marina* can also be found at the surface in dense patches, this being recorded during the day in the Caribbean (Owre and Foyo 1976), as well as at night in the eastern Gulf of Mexico (present study). The "midnight sinking" observed here has not previously been reported for *E. marina* or for any other member of the genus. The "midnight sinking" was absent in stages younger than copepodid V.

The apparent "midnight sinking" seen in the population has been shown to occur in chaetognaths (Pearre 1973) and a model was proposed in which the diel vertical migration of *Sagitta elegans* was influenced by a positive phototaxis and a light-controlled geotaxis. It was suggested that feeding satiation also influenced this balance and caused "midnight sinking" of *S. elegans* individuals with full guts. The feeding data in the present study suggest that "midnight sinking" in *E. marina* may also be influenced by the degree of satiation in the population. Feeding activity in adult females based on incidence of relatively full guts (*i.e.*, categories 2-4 fullness, Fig. 3) appears higher before sinking occurs, and the apparent movement away from the surface of the population center may be the result of many members of the population either actively or passively descending to deeper waters after successful feeding. Nearly a 2-fold increase in microzooplankton is encountered in moving from 50 to 30 meters (Hopkins 1982). The pre-dawn ascent in the population would allow those individuals to feed again in more food-rich waters before returning to daytime depths. Our data show an increase in stomach fullness in adult females just prior to the dawn descent (Figs. 2 and 3).

Copepodid IV and younger stages showed low levels of feeding throughout the night including the period when adult females and other older stages were undertaking the midnight descent. This suggests that ingestion is less cyclic and feeding to satiation may occur to a lesser degree in the juvenile stages. This may offer a possible explanation for the lack of an apparent midnight descent in the younger stages (see Fig. 4B).

Several theories have been proposed to explain the adaptive value of vertical migrations (see McLaren 1963, Angel 1984, for reviews). Among the proposed ideas is that vertical migrations occur in order to provide mechanisms for horizontal dispersal of a population (dispersing of the gene pool) and to reduce from three dimensions to two the space necessary to search for mates. Both of these considerations have application to *E. marina* in this study. Variations in current shears in this environment will result in dispersion of this population where only some of the population migrates at any given time, and where ontogenetic differences exist in migratory behavior. There is some indication in our data that synchronous migrations also occur among reproductively active individuals to enhance contact for mating. The surface swarm collected in one of our night samples corroborates this

suggestion in that the swarm showed a higher percentage of adults than in other shallow collections. Even though the male:female (1:2) ratio remained the same as elsewhere, there was a noticeably higher occurrence of females with attached spermatophores and males with spermatophores extruded on the fifth leg. Since adult males do not feed, reproduction would be the most obvious reason for their migration to the surface.

The most compelling reasons for migration in *E. marina* in this study are those of food availability and avoidance of visual predation. The former is discussed above. As to the latter, visual acuity of predators declines with diminishing light levels and hence increasing depth. *E. marina* should select a daytime depth where its perceptible visual cues to predators are minimal. Whether this is true for this species remains to be examined.

Diet Composition and Predation Impact

The diet of *Euchaeta marina* is reflected in its feeding appendages. This species, as typical of the genus, has large maxillipeds with long, stout setae that appear poorly suited for filtration. These appendages indicate feeding modes involving the capture of large particles and carnivory. The data on diet composition support this conclusion in showing that adult females fed exclusively on small copepods and other crustaceans as has been found for other members of the genus (Wickstead 1962, Mullin 1966, Harding 1974, Hopkins 1985). Among the small crustacean food, recognizable prey items belonged to a variety of prey types (*e.g., Oncaea, Microsetella,* and *Corycaeus*). Based on the size distribution of these prey at the sample site and on their occurrences in the guts (Table 3), these prey mostly belong in a size class of less than one mm. Yen's (1982) data on *Euchaeta elongata*, a 4.0 mm species, showed a preference for prey smaller than 1 mm (*Pseudocalanus* spp., 0.95 mm body length). Based on this ratio of predator to prey size, we would expect the optimum prey size for *E. marina* to be 0.8 mm. The number of small metazoan plankton in the size range (up to 1 mm) ingested by *E. marina* was estimated to be 30 to 35 times more abundant than > 1 mm zooplankton in the eastern Gulf of Mexico, with 94 of the numbers of the < 1 mm zooplankton being concentrated in the upper 200 meters (Hopkins 1982). The data also indicate that a maximum in numbers and biomass of this size fraction occurs at 25 meters. The initial ascent of *E. marina* at dusk to near 30 meters correlates with the vertical distribution of this small prey.

Our data indicate that adult males of *Euchaeta marina* do not feed. This has been shown in adult males of two other species, *Euchaeta scotti* (Mullins 1966) and *E. antarctica* (Hopkins 1987), and in the males of species of several other copepod genera as well, *e.g., Calanus tenuicornis, Gaetanus (Gaidius) brevispinus,* and *Scaphocalanus magnus* (Mullin 1966).

In experiments with adult female *E. norvegica* fed a mixture of natural prey, average ingestion rates were less than one individual per day (Bamstedt and Holt 1978). Adult female *E. elongata*, however, showed higher capture rates (0.67-3.18 prey•predator^{-1}•day^{-1}), (Yen 1982). In the present study usually only

one prey individual was recognizable, with a maximum of three items. Other unidentifiable food material, however, was also observed. A rough estimate of capture rates is possible through energetics modeling. Daily metabolic needs of adult female *Euchaeta marina* can be gauged from existing metabolic data on this species and its congeners. Respiration rates for adult female *Euchaeta marina* run at experimental temperatures (28.0 - 29.2° C) similar to those at the study site range from 2.24 to 2.69 μL O_2•animal^{-1}•hour^{-1}(x = 2.47 μL O_2•animal^{-1}•hour^{-1}, Ikeda 1970). Assuming an oxycaloric equivalent of 4.7 Kcal•liter O_2^{-1}, (Gordon 1977), the daily metabolic needs of adult females can be estimated as 2.79×10^{-4} Kcal•day^{-1}. Similarly, the energy yield of prey items can also be estimated from available data. Average dry weights for small (< 1.0 mm) calanoids at the study site were estimated at 0.010 mg. Assuming that Gulf of Mexico crustaceans contain 60% protein, 38% fat and 2% carbohydrates on a dry weight basis, and that the caloric content of protein, fat, and carbohydrate are 4.5, 9.5, and 4.0 Kcal•gm^{-1}, respectively, (Gordon 1977), then the caloric yield of an average small (< 1.0 mm) calanoid is approximately 6.40×10^{-5} Kcal. Based on these calculations, an adult female would have to consume at least four of these prey per day or 0.040 mg dry weight of crustacean prey to meet respiratory demands alone. These calculations suggest that *E. marina* may feed during each of the peak periods shown in Figure 3B, or that they capture more than one prey item during each feeding period. Occurrences of unidentified food in guts is some evidence of multiple prey captures and for multiple feeding periods in this species.

The impact of *Euchaeta marina* on the available resources at the study site also can be estimated, within broad limits, from feeding data. Assuming minimum ingestion rates of 2 to 4 1.0 mm prey/day for adults and copepodid V individuals and from 1 to 2 prey/day for copepodid IV and earlier composite individuals, then the population would be removing at least 1990 to 3980 prey per day in the upper 100 meters. Crustaceans < 1.0 mm body length in the upper 100 meters average 852,000 m^2 in the eastern Gulf of Mexico (Hopkins, unpublished data). *E. marina*, then, is potentially capable of removing at least between 0.23 and 0.47% of the available microcrustacean resources in the upper 100 meters daily, with the grazing impact being greatest at the centers of abundance of *Euchaeta marina*. These ingestion rates are based on minimum needs to meet respiration demands. More or larger prey would have to be consumed than these numbers indicate if growth and reproduction are to be achieved. Also, the numbers of copepodid stages IV and smaller *E. marina* undoubtedly have been underestimated as a result of escapement. Because of these factors our value for predation impact is probably low. If it were off by as much as 100%, however, the rate of impact would still be less than 1% of the available crustacean resources < 1.0 mm in size per day. If it is assumed that the crustacean microzooplankton replacement time is at least every 2-6 weeks in tropical-subtropical waters then the impact of this one species on available food resources indeed seems small, despite the relative abundance of *E. marina* in the epipelagic layers. The zooplankton community is diverse at low latitudes, however, with approximately 200 species of

copepods alone (Owre and Foyo 1967), many of these being omnivorous or predacious. If as Hayward and McGowan (1979) suggest, zooplankton populations at tropical-subtropical latitudes are principally predator controlled, then predator pressure has to be considered incrementally in terms of the cumulative effect of many carnivore-omnivore species.

ACKNOWLEDGMENTS

We would like to thank Norman J. Blake for providing materials and advice for the histological aspect of this study, and Joseph H. Torres for providing valuable ship time for some of these samples. We also thank V.E. Shuert for her help with the preparation of this manuscript. This research in part was supported by NSF Grant OCE 75-03845.

LITERATURE CITED

ANGEL, M.V. 1984. Vertical migrations in the oceanic realm: possible causes and probable effects. *Contributions in Marine Science.* **27(Supplement)**:45-70.

BAIRD, R.C. and T.L. HOPKINS. 1981. Trophodynamics of the fish *Valenciennellus tripunctulatus*. II. Selectivity, grazing rates, and resource utilization. *Marine Ecology - Progress Series.* **5**:11-19.

BAMSTEDT, U. and M.R. HOLT. 1978. Experimental studies on the deep-water pelagic community of Korsfjorden Norway. Prey size preference and feeding of *Euchaeta norvegica* (Copepoda). *Sarsia.* **63**:225-236.

BENNETT, J.L. 1986. Vertical distribution, abundance and feeding of the copepod genus *Pleuromamma* in the Eastern Gulf of Mexico. Masters Thesis. University of South Florida, St. Petersburg.

GEINRIKH, A.K. · 1958. On the nutrition of marine copepods in the Tropical Region. *Doklady, Akademiya Nauk SSSR.* **119**:229-233.

GORDON, M.S. 1977. *Animal Physiology: Principles and Adaptions.* 3rd edition. Macmillan Publishing Co., Inc. New York. 699 p.

HARDING, G.C.H. 1974. The food and feeding of the deep-sea copepods. *Journal of the Marine Biological Association, U.K.* **54**:141-155.

HAYWARD,T.L. and J.A. McGOWAN. 1979. Pattern and structure in an oceanic zooplankton community. *American Zoologist.* **19**:1045-1055.

HEFFERNAN, J.J. and T.L. HOPKINS. 1981. Vertical distribution and feeding of the shrimp genera *Gennades* and *Bentheogennema* (Decapod:Penaeidea) in the eastern Gulf of Mexico. *Journal of Crustacean Biology.* 1:461-473.

HOPKINS, T.L. 1982. The vertical distribution of zooplankton in the eastern Gulf of Mexico. *Deep Sea Research.* **29**:1069-1083.

_____. 1985. Food web of an Antarctic midwater ecosystem. *Marine Biology.* **89**:197-212.

_____. 1987. The midwater food web in McMurdo Sound, Ross Sea, Antarctica. *Marine Biology* (in press).

_____, J.L. BENNETT, and P.G. SHUERT. 1979. Zooplankton study at the Florida west coast O.T.E.C. Site. A final report to the Lawrence Berkeley Laboratory. 41 pp.

_____ and R.C. BAIRD. 1975. Net feeding in mesopelagic fishes. *Fishery Bulletin* **73**:908-914.

_____ and _____. 1977. Aspects of the feeding ecology of oceanic midwater fishes. pp 325-360. In N. Anderson and B.J. Zahuranec (eds) *Proceedings of the International Symposium on Prediction of Sound Scattering in the Ocean.* Plenum Press, New York.

_____ and _____. 1981. Trophodynamics of the fish *Valencienellus tripunctulatus*. I. Vertical distribution, diet and feeding chronology. *Marine Ecology - Progress Series.* **5**:1-10.

_____ and _____. 1985a. The feeding ecology of four hatchetfishes (Sternoptychidae) in the eastern Gulf of Mexico. *Bulletin of Marine Science.* **36**:260-277.

_____ and _____. 1985b. Aspects of the trophic ecology of the mesopelagic fish *Lampanyctus alatus* (Family Myctophidae) in the eastern Gulf of Mexico. *Biological Oceanography.* **3**:285-313.

_____, _____ and D.M. MILLIKEN. 1973. A messenger-operated closing trawl. *Limnology and Oceanography.* **18**:488-490.

_____ and T. LANCRAFT. 1984. The composition and standing stocks of mesopelagic micronekton at 27°N 86°W in the eastern Gulf of Mexico. *Contributions in Marine Science.* **27**:143-158.

IKEDA, T. 1970. Relationship between respiration rate and body size in marine plankton animals as a function of the temperature of habitat. *Bulletin of the Faculty of Fisheries, Hokkaido University.* **21**:91-112.

LEAVITT, B.B. 1938. The quantitative vertical distribution of macrozooplankton in the Atlantic Ocean Basin. *Biological Bulletin, Marine Biological Laboratory, Woods Hole.* **74**:376-394.

LONGHURST, A.R. 1976. Interactions between zooplankton and phytoplankton profiles in the eastern tropical Pacific Ocean. *Deep Sea Research.* **23**:729-754.

McGOWAN, J.A. 1974. The nature of oceanic ecosystems. pp. 9-28 in C.B. Miller (ed) *The Biology of the Oceanic Pacific.* Oregon State University Press, Corvallis.

McLAREN, I.A. 1963. Effects of temperature on the growth of zooplankton, and the adaptive value of vertical migration. *Journal of the Fishery Research Board of Canada.* **20**:685-727.

MORRIS, M.J. and T.L. HOPKINS. 1983. Biochemical composition of the crustacean zooplankton from the eastern Gulf of Mexico. *Journal of Experimental Marine Biology and Ecology.* **69**:1-19.

MULLIN, M.M. 1966. Selective feeding by calanoid copepods from the Indian Ocean. pp. 545-554. In H. Barnes (ed) *Some Contemporary Studies in Marine Science.* George Allen and Unwin Ltd., London.

OWRE, H.B. and M.FOYO. 1967. *Copepods of the Florida Current. Fauna Caribaea, No. 1.* Institute of Marine Science, University of Miami, Florida. 137 p.

_____ and _____. 1976. *Caribbean Zooplankton. Part 1 - Siphonophora, Heteropoda, Copepoda, Euphausiacea, Chaetognatha and Salpidae.* Office of Naval Research, Department of the Navy. 712 p.

PEARRE, S. 1973. Vertical migration and feeding in *Sagitta elegans* Verrill. *Ecology.* **54**:300-314.

_____. 1979. Problems of detection and interpretation of vertical migration. *Journal of Plankton Research.* **1**:29-44.

ROE, H.J.S. 1972. The vertical distribution and diurnal migrations of calanoid copepods collected on the Sond Cruise, 1965. II. Systematic account: families Euchaetidae up to and including the Metridiidae. *Journal of the Marine Biological Association, U.K.* **52**:525-552.

ROEHR, M.G. and H.B. MOORE. 1965. The vertical distribution of some common copepods in the Straits of Florida. *Bulletin of Marine Science.* **15**:565-570.

VERVOORT, W. 1963. Pelagic Copepoda I. *Atlantide Report.* **7**:77-194.

VINOGRADOV, M.E. 1970. Vertical distribution of the oceanic zooplankton. Translation of monograph **TT 69-59015**. 346 p. Reference in *United States Government Research and Development Reports* **70**. 64 p.

WICKSTEAD, J.H. 1962. Food and feeding in pelagic copepods. *Proceedings of the Zoological Society, London.* **139**:545-555.

YEN, J. 1982. Sources of variability in attack rates of *Euchaeta elongata* Esterly, a carnivorous marine copepod. *Journal of Experimental Marine Biology and Ecology.* **63**:105-117.

Contributions in Marine Science. (1987) Vol. 30:63–76.

THE IMPORTANCE OF BEHAVIORAL AND BIOCHEMICAL DIFFERENCES BETWEEN FIDDLER CRAB TAXA, WITH SPECIAL REFERENCE TO *UCA RAPAX* (SMITH) AND *U. VIRENS* (SALMON AND ATSAIDES)

Michael Salmon and Michelle K. Kettler[1]

Department of Ecology, Ethology, and Evolution
University of Illinois
Shelford Vivarium
606 E. Healey Street
Champaign, IL 61820

ABSTRACT

The fiddler crab *U. rapax* is a tropical species which ranges northward to the East and West coast of Florida. It is replaced on the Gulf of Mexico by a temperate form, *U. virens*, which it closely resembles in structure. We compared the two taxa biochemically at 21 loci and found them virtually indistinguishable. However they showed distinct differences in male pre-mating (visual and vibrational) displays. These characters, in addition to those reported by others (differences in hemolymph amylases and ability to acclimate to colder temperatures) indicate that the two forms are sibling species which have probably diverged relatively recently (within 50 thousand years).

Comparisons between the premating displays of other structurally similar fiddlers show similar magnitudes of behavioral difference but genetic divergence is much more pronounced. Thus, behavioral differences apparently can arise in advance of genetic ones, probably as a consequence of intersexual selection for arbitrary characteristics of male display.

INTRODUCTION

Fiddler crabs (Genus *Uca*) are abundant in temperate salt marshes (Montague 1980), as well as subtropical and tropical intertidal communities throughout the world (Crane 1941, 1943; Macnae 1968; Icely and Jones 1978). In her treatise on the group, Crane (1975) recognized 62 species but extensive collections and surveys in other locales have led to the description of several new taxa (*e.g.*, George and Jones 1982) and to range extensions for several established species (Barnwell and Thurman 1984). In most cases, morphological differences between species allow for their clear taxonomic separation but as in many speciose groups, some taxa diverge in ecology, physiology and behavior while showing little structural change. Such physically indisting-

[1] Department of Biology, University of Wisconsin, Eau-Claire, WI 54701.

uishable forms are well known among arthropods (*e.g.*, Crozier 1983) and often pose problems for taxonomists working with preserved material.

Species difficult to separate morphologically are not uncommon among decapod crustaceans (Knowlton 1986). Knowlton distinguished between "sibling" species, which are closely related genetically and morphologically similar (*e.g., Panopeus* species "complex": Turner and Lyerla 1980; Williams 1983; Sullivan, Miller, Singleton, Scheer and Williams 1983; *Alpheus* "complex": Knowlton and Bert, forthcoming) and "cryptic" species which are also structurally similar but whose genetic affinities are not particularly close (some *Uca*: Salmon, Hyatt, McCarthy and Costlow 1978; some *Trapezia*: Huber 1985) or are unknown.

Several species of fiddler crabs found along the U.S. Gulf of Mexico coast closely resemble species which are found elsewhere in the United States or in the Caribbean. *Uca virens*, a Gulf coast species, was originally distinguished from a structurally similar east coast species, *U. pugnax*, by its unique male premating displays ("waving" patterns of the enlarged claw; temporal patterns of vibrational signals; Salmon and Atsaides 1968a). Salmon and Atsaides (1968b) also described differences between the premating displays of *U. virens* and its other close relatives (*U. longisignalis, U. rapax, U. burgersi*) found in the United States. Selander, Johnson and Avise (1971) showed that *U. virens* is distinct genetically from *U. pugnax, U. minax*, and *U. longisignalis*, and that each of these species is a genetically distinct entity.

Von Hagen (1975) could find no structural characters to distinguish *U. virens* from *U. rapax*, although Barnwell and Thurman (1984) found that these two forms differed in mobility of hemolymph amylases. They deemed this evidence insufficient to justify separation into distinct taxa and therefore considered the northward range of *U. rapax* to encompass those temperate locales reported to be occupied by *U. virens*. However, *U. rapax* is a tropical species known for its inability to acclimate to colder temperatures and to survive at temperate latitudes (Vernberg 1959a, 1959b; Vernberg and Tashian 1959; Miller and Vernberg 1968).

In this paper, we address two issues. First, we compare the behavior of *U. rapax* and *U. virens* and supplement the available data (Salmon 1967; Salmon and Atsaides 1968b; Salmon 1971) on their premating displays. Second, we analyze their differences in electromorph mobilities to determine if these are sibling or cryptic species. Finally, we summarize evidence demonstrating that ethological data are useful for distinguishing between these and other structurally similar fiddler crab taxa.

METHODS

Behavioral Analyses

The techniques used to record and analyze male fiddler crab displays have been described elsewhere (Hyatt 1977; Salmon, Ferris, Johnston, Hyatt and Whitt 1979). Briefly, male visual courtship consists of extensions and retractions ("waving" displays) of the enlarged claw. In *U.*

rapax and *U. virens*, extensions and retractions are embellished by "jerks" whose number and duration constitute important species-typical temporal features (Crane 1975). Displays were recorded on film or video tape when the male faces the camera. Temporal data are taken by counting film frames (or video sweeps) from the beginning to the end of the display. We measured the number of jerks per wave and the duration of each jerk (onset of one jerk to the onset of the next) within each of four consecutive waves shown by single crabs.

Acoustical signals are detected with accelerometers or contact microphones and recorded on tape. They are then analyzed from traces made on a storage oscilloscope and measured directly from the screen. These signals usually consist of two or more "pulses" separated from one another by a relatively short interval. A cluster of closely spaced pulses is called a "sound;" consecutive sounds are separated by wider intervals than those between pulses. Species reliably differ in one or more of the following temporal properties of their vibrational signals: number of pulses per sound, sound duration, pulse repetition rate and intervals between consecutive sounds (Salmon *et al.* 1978; Salmon *et al.* 1979).

For *U. virens*, our sample of vibrational signals consisted of recordings from Texas (n = 2 males), Mississippi (n = 3) and Louisiana (n = 2) obtained during the summer of 1967. Waving displays were filmed during August (1985) from four crabs (1.10-1.60 cm carapace width) found in Ochlockonee, Florida, filmed at 18 fps using a super 8 camera and telephoto lens. All subjects were waving at "medium" intensity (unstimulated by nearby moving females). The first four consecutive waves produced by each male were used for detailed analysis. Air temperatures during filming ranged from 27-30°C.

Uca rapax occurs on the East and West coast of Florida (Salmon 1967). Our samples consisted of crabs from both coasts (Fort Pierce, summer of 1985; Osprey and Sarasota, summers of 1966 and 1985, respectively). Vibrational displays were recorded from five crabs from each coast. All recordings were obtained within 10 minutes after the onset of sound production, some 45-60 minutes after sunset. The first ten consecutively produced sounds per male were chosen for analysis, as described above for *U. virens*. Air temperatures ranged from 21-25°C. Waving samples were obtained from 4 males (1.40-2.01 cm carapace width) filmed at Sarasota and 4 at Ft. Pierce. Again, the first four consecutive medium intensity waves were selected for analysis. Air temperatures during filming ranged from 29-32°C.

Statistical analyses of the differences between displays were based upon formulae given in Siegel (1956) and Zar (1984).

Electrophoretic Analyses

Electromorph analyses were based upon 15 *U. rapax* from Fort Pierce, 15 from Sarasota, and 15 *U. virens*, from Ochlockonee, FLorida. Individuals were examined for isozyme patterns at 21 loci (Table 1). Skeletal leg muscle or viscera were homogenized in 0.2 ml of 0.1 Tris-HCl, ph 7.0 at 4°C, with a Potter Elvejhem pestle. Extracts were centrifuged for 20 minutes at 27,000 × g at 4°C. The super,natants were then subjected to electrophoresis in starch gels (Sigma starch, lot 45E-0282 or 85F-0421). Staining procedures were as described in Kettler and Whitt (1986). Genetic distances between each of the three samples (East coast, West coast *U. rapax; U. virens*) were determined by the method of Nei (1978).

RESULTS

Premating Displays

The vibrational signals of *Uca rapax* from each coast showed no differences in the number of pulses per sound ($X^2 = 0.01$, $p > 0.20$) or in sound duration ($X^2 = 1.49$, $p > 0.20$; median tests corrected for continuity; Fig. 1). However, comparison of the number of pulses per sound and the sound duration shown by *U. virens* and both populations of *U. rapax* (pooled) revealed highly

TABLE 1

Enzymes, nomenclature, tissue sources and electrophoretic conditions used in this study.

Enzyme system	Locus abbreviation	EC number	Tissue source	Buffer system
Aspartate amino-transferase	Aat-1,2	2.6.1.1	muscle	TC*
Esterase	Est-1,2,3	3.1.1.1	viscera	EBT**
Glucose phosphate isomerase	Gpi	5.3.1.9	viscera	EBT
Glutamate dehydrogenase	Gdh	1.4.1.2	muscle	TC
Glycerol-3-phosphate dehydrogenase	G-3-pdh	1.1.1.8	muscle	TC
Isocitrate dehydrogenase	Idh-1,2	1.1.1.41	muscle	TC
Lactate dehydrogenase	Ldh	1.1.1.27	muscle	TC
Malate dehydrogenase	Mdh-1,2,3	1.1.1.37	muscle	TC
Mannose phosphate isomerase	Mpi	5.3.1.8	muscle	EBT
6-Phosphoglucate dehydrogenase	6-Pdg	1.1.1.44	muscle	TC
Phosphoglucomutase	Pgm	2.7.5.11	muscle	TC
Protein	Prot-1,2	--------	muscle	TC
Superoxide dimutase	Sod-1,2	1.15.1.1	viscera	EBT

* Tris-Citrate, pH 7.0 (Whitt 1970).
** Tris-EDTA-borate, pH 8.6 (Wilson, Whitt and Prosser 1973).

significant differences ($X^2 = 145$, $p < 0.001$ for pulses; $X^2 = 64.4$, $p < 0.001$ for durations). Salmon and Atsaides (1968b) showed that *U. virens* produces only

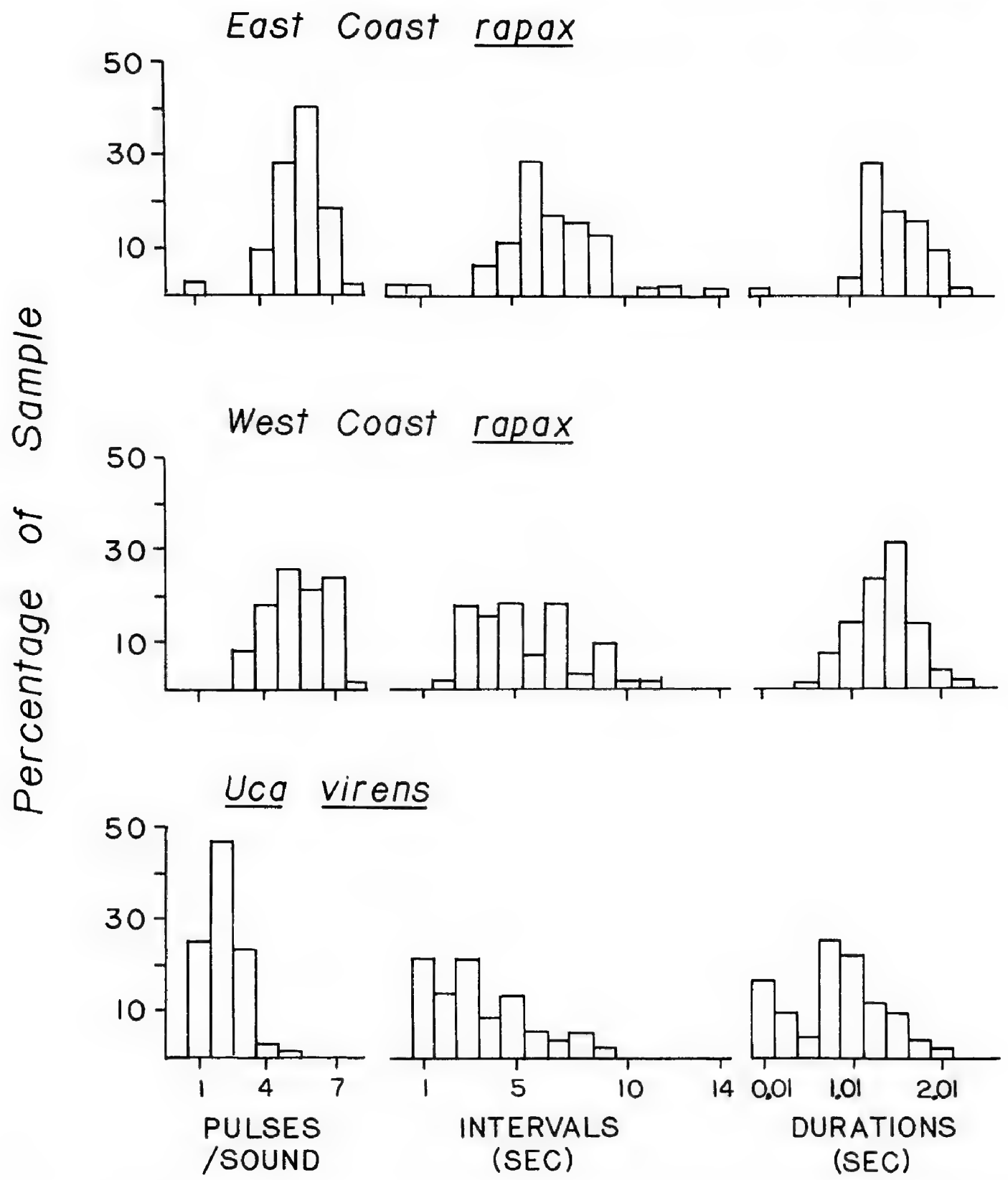


FIG. 1. Distribution of vibrational characters for *Uca rapax* and *U. virens*. Data are based upon 10 consecutively produced sounds per crab for five crabs from each coast for the former and 10 or more sounds (from 7 crabs) for the latter.

a few (1-3) short pulses in its sounds while typical sounds of *U. rapax* contain several (4-7) longer pulses. The distribution of intervals between consecutive sounds produced by *U. virens* was significantly shorter than those between consecutive sounds of East coast *U. rapax* ($X^2 = 16.1, p < 0.001$), but not West coast *U. rapax*, indicating that the spontaneous rate of "calling" in *U. virens* was often more rapid than in *U. rapax*.

Pulse repetition rates/sec (mean ± SD) were 3.53 ± 0.49 for East coast *U. rapax*, 3.69 ± 0.79 for West coast *U. rapax* and 2.11 ± 0.25 for *U. virens*. An ANOVA revealed significant differences among the means ($F = 60.58$, $p < 0.05$). Further analysis (using a Tukey test) showed that whereas pulse repetition rates were similar for *U. rapax* from both coasts, those for both populations of *U. rapax* were significantly faster than those shown by *U. virens*. Thus *U. rapax* and *U. virens* exhibited differences in three of four measured parameters of their vibrational displays.

Waving display durations (mean ± SD) (Table 2) ranged from 4.52 ± 1.48 seconds for *U. virens* to 6.09 ± 0.85 seconds for East coast *U. rapax*. These differences were statistically significant (one-way ANOVA, $F = 5.60$, $p < 0.05$). Again, a Tukey test indicated no differences between the two populations of *U. rapax*, but waving duration of *U. virens* were significantly shorter than those of East coast *U. rapax*.

Patterns of jerking during waves by *U. virens* differed from both populations of *U. rapax* while those shown by *U. rapax* from both coasts were statistically identical (Table 2). *Uca rapax* showed about twice the number of jerks during waving extension, each of which lasted less than half as long as those shown by *U. virens*. Return portions of the wave were usually accomplished with two (or rarely, three) jerks in *U. rapax* but uniformly with one jerk in *U. virens* (Fig. 7 in Salmon and Atsaides 1968b). Finally, the return movement of the claw took 0.82-1.02 seconds for *U. rapax* but averaged 0.44 seconds for *U. virens*.

Electrophoretic Results

Of the 21 loci examined, 14 were fixed for the same allele in both species and 7 were polymorphic (Table 3). With the exception of two loci (esterases 1, 2) which showed small differences in allelic frequencies, all other polymorphic variation was negligible. Nei genetic distances between the three groups were: E *vs.* W coast *U. rapax* = 0.016; E coast *U. rapax vs.* U. virens = 0.010; W coast *U. rapax vs.* U. virens = 0.035.

DISCUSSION

Biochemical Differences

Our analysis indicates that *U. virens* and *U. rapax* show little evidence of genetic differentiation. Two-thirds of the loci were fixed for the same allele. For those loci which were polymorphic, allelic frequencies were similar though genetic distances between west coast *U. rapax* and *U. virens* were somewhat greater than those between east coast *U. rapax* and *U. virens*. The lack of biochemical differences was surprising as the loci sampled have clearly separated other morphologically similar fiddler crabs (Selander *et al.* 1971, Salmon *et al.* 1979), as well as other decapods (Turner and Lyerla 1980,

TABLE 2

Temporal patterns (mean ± SD) of waving display shown by *Uca rapax* from the east and west coasts of Florida, and by *U. virens* from northwestern Florida. N = 4 waves/male from each of 4 males/sample (16 waves/sample). Values are in seconds.

Character	*Uca rapax* **(East)**	*Uca rapax* **(West)**	*Uca virens*
Wave Duration	6.09 ± 0.85	4.89 ± 1.71	4.52 ± 1.48
Extend: Number Jerks	17.69 ± 2.21	14.81 ± 5.52	7.25 ± 2.14
Return: Number Jerks	2.44 ± 0.63	2.06 ± 0.44	1.00 ± 0.00
Extend: Jerk Duration	0.28 ± 0.072	0.28 ± 0.068	0.56 ± 0.20
Return: Jerk Duration	0.42 ± 0.13	0.40 ± 0.10	0.44 ± 0.11

Huber 1985). For the present, clear biochemical separation between the species rests upon Barnwell's (in Barnwell and Thurman 1984) survey of hemolymph amylases. Two forms of the enzyme were distinguished. The slower migrating form was characteristic of crabs collected in temperate locales where *U. virens* is found exclusively (East Texas to northwestern Florida). The faster migrating electromorph was characteristic of populations to the South, where *U. rapax* is found exclusively (Miami, Florida; the Yucatan peninsula, Colombia and Brazil). Obviously, such differences between a continuously distributed population could not occur if its members were interbreeding.

The evidence presently available, then, suggests that the two forms are sibling species, so recently differentiated that there has been insufficient time for the accumulation of significant genetic differences. This hypothesis is supported by the specific enzyme systems which have diverged. Esterases and blood proteins are rapidly evolving electromorphs tracking changes in genes over as short a period as 20-50 thousand years (*e.g.*, Sarich 1977).

Behavioral Divergence and Taxonomy

Crane (1941) first recognized that the waving displays of fiddler crabs were species-typical movements. Comparative studies by Altevogt (1966, 1970), and reviews by von Hagen (1975) and Salmon (1967) showed that the vibrational signals of males also varied from one species to the next in spectral energy distribution and temporal pattern. The two types of displays

TABLE 3

Frequencies of electromorphs at polymorphic loci found in *Uca rapax* from the east and west coasts of Florida, and in *U. virens* from northwestern Florida (N = 15 crabs/sample).

Enzyme	*Uca rapax* (East)	*Uca rapax* (West)	*Uca virens*
Esterase-1	A = 0.967 B = 0.033	A = 1.000 B = 0.000	A = 1.000 B = 0.000
Esterase-2	A = 0.733 B = 0.267 C = 0.000	A = 0.766 B = 0.233 C = 0.000	A = 0.533 B = 0.100 C = 0.367
Esterase-3	A = 0.633 B = 0.367	A = 0.677 B = 0.333	A = 0.467 B = 0.533
Glycerol-3-phosphate dehydrogenase	A = 0.967 B = 0.033 C = 0.000	A = 0.967 B = 0.000 C = 0.033	A = 1.000 B = 0.000 C = 0.000
Glucose phosphate isomerase	A = 0.567 B = 0.000 C = 0.433	A = 0.500 B = 0.167 C = 0.333	A = 0.600 B = 0.200 C = 0.200
Isocitrate dehydrogenase-2	A = 1.000 B = 0.000	A = 0.800 B = 0.200	A = 1.000 B = 0.000
Protein-2	A = 0.967 B = 0.033 C = 0.000	A = 0.967 B = 0.000 C = 0.033	A = 1.000 B = 0.000 C = 0.000

are also functionally linked; each serves as sexual attractants ("calling" signals) during the day (waving) or at night (vibration; reviewed in Salmon and Atsaides 1968b). Of the greatest importance, differences between species in their vibrational and visual displays are genetically determined (Salmon and Hyatt 1979) and are correlated with specific patterns of mate choice by females (Salmon et al. 1978). Not surprisingly, then, display differences have consistently provided reliable criteria for separating morphologically similar species (Table 4). In each case, behavioral conclusions have ultimately been corroborated by relevant biochemical genetic data.

Why, then, have morphological taxonomists been reluctant to accept conclusions based upon ethological (sexual display) characters? In part, it is because behavioral data cannot provide a means for sorting previously collected material (Knowlton 1986) and in that sense fail to resolve past identification problems. Another reason is that some taxonomists are so deeply committed to diagnoses based upon structure that conclusions based upon other criteria are ignored. For example, Barnwell and Thurman (1984) claimed that all the species described by Salmon from the Gulf coast were not

TABLE 4

Differences between premating displays of morphologically similar male fiddler crabs. All pairs, with the exception of *Uca virens* and *U. rapax*, are cryptic species.

Species Pairs (Reference)	Wave Duration (s)	Wave "Form"	Pulses/ Sound (typically)	Sound Duration (s)	Pulses per s (typically)
Uca speciosa	~0.48	Minor chela and	3-4	Both similar	5-6
Uca spinicarpa	~1.07	leg movements	5-10	(0.5-0.8)	10-11
(Salmon *et al.* 1979)		differ			
Uca pugilator	Both	Chelae and leg	5-10	Both similar	8-13
Uca panacea	similar	movements differ	8-27	(0.5-0.8)	21-26
(Salmon *et al.* 1978)	(1.0-1.3)				
Uca virens	Both	"Jerking" patterns	1-3	0.2-1.5	2
Uca rapax	similar	differ	4-7	1.0-2.0	3-4
(this study)					
Uca mordax	Both	"Jerking" Patterns	10-22	1.5-2.5	~7
Uca burgersi	similar	differ	2-6	3.0-4.0	~1
(von Hagen 1983, 1984)*	(4.0-4.2)				

* All values for sound comparisons are approximations as different units were measured. These species also differ in mechanism employed to produce their calling sounds ("rapping" in *U. mordax*; "honking" in *U. burgersi*).

compared to sympatric associates with which they might be confused. In fact, the comparisons were made (Salmon and Atsaides 1968b) but since they were ethological rather than structural, the studies were criticized ". . . for ignoring standard taxonomic principles." Barnwell and Thurman cited Felder (1973), von Hagen (1975) and Crane (1975) as concluding that the ethological data were too variable to be of diagnostic value. However, neither Crane nor von Hagen ever compared the published behavioral data (Figs. 7 and 9 in Salmon and Atsaides 1968b, Salmon 1971) to demonstrate its lack of utility nor did they present new behavioral data to quantify its "variability." Felder's (1973) taxonomic conclusions were based upon the unsubstantiated belief that behavioral differences between *U. pugnax* and *U. virens* (the taxa originally confused) constituted inadequate evidence for their separation, and von Hagen's (1970) earlier assessments. Two years later, von Hagen (1975) determined that *U. virens* could in fact be morphologically distinguished from *U. pugnax*. However, he (and eventually Barnwell and Thurman) then discovered that it was impossible to structurally separate *U. virens* from *U. rapax*. As we have shown, these two taxa are easily distinguished on the basis of behavior.

Even when non-morphological data distinguish unambiguously between species, their importance has been minimized. For example, Crane (1975) synonymized two species (*U. spinicarpa* and *U. speciosa*), originally distinguished by Rathbun (1918), because she could find no reliable morphological differences between them. However, the two forms were found to differ in genetic constitution (Nei index of 0.70) and premating displays (Salmon *et al.* 1979). Although this study resolved the issue, Barnwell and Thurman stated that its conclusions were "...somewhat overdrawn..." because the two forms "...were merely restored to the status assigned them on morphological grounds more than 60 years earlier by Rathbun." Barnwell and Thurman missed the point, however, which was that two competent morphological taxonomists had reached opposite conclusions based upon structure, whereas ethological and biochemical evidence led to an unambiguous resolution.

Ethological Comparisons and Diagnostic Characters

We have argued here that ethological characters can be valid descriptors of differences between taxa. It must be emphasized, however that if behavioral data are to be useful in fiddler crab taxonomy, they must be correctly gathered and analyzed. Even where morphologically similar species differ in their acoustic and visual displays (Table 4), the characters involved in those displays vary in diagnostic utility. For example, wave or sound duration separate only some species pairs, and other characters overlap in their distributions (*e.g.* pulses/sound) even though mean values differ statistically. However wave "form" and sound pulse repetition rate clearly distinguish between all cryptic and sibling species thus far studied. Significantly, these are the display parameters to which the crab receptor systems seem most sensitive and are therefore likely to convey information. For example, Hall (unpublished observation) found that each jerk within a wave (but not the pauses between jerks) evoked vigorous ERG responses from the eye of *U. minax*. The onset of each vibrational pulse and, to a lesser extent, the pulse amplitude modulation "envelope," elicited strongest responses from vibration-sensitive interneurons (Hall 1985).

Variability within samples of displays can be greatly reduced if some effort is made to control for differences in display "intensity." We define displays given at "medium" intensity as those shown by males when motivated to wave or produce sound repeatedly, but not influenced to do so by movements from nearby females. These precautions reduce the most significant cause of variation in male display intensity but do not eliminate the behavior of neighboring males, whose courtship activity is also stimulating, though less so (Salmon 1965). Such efforts to standardize samples preserve the essential differences shown between species and enhance their utility as sensitive discriminators. These procedures also eliminate the possibility that the displays of one taxon when males are sexually stimulated by females will be

compared to another when they are not, leading to false conclusions regarding real differences in behavior.

We also standardized our behavioral samples by collecting data at times in the lunar cycle when males were actively displaying. Almost all male fiddler crabs show semimonthly rhythms of display activity which are linked temporally to female receptivity cycles (reviewed in Christy 1978, 1982). Behavioral observations should be timed to coincide with peaks of these periodicities, even if the taxa in question exist allopatrically where tidal regimes may differ in phase or in semimonthly pattern.

Speciation Processes and Zoogeography

In an earlier study. *U. virens* was described as ranging in the United States from Port Aransas, Texas to Ocean Springs, Mississippi (Salmon and Atsaides 1968a). Here, we report crabs at Ochlockonee (Apalachee Bay), Florida though they were never abundant. There is agreement that *U. rapax* occurs as far North on the West coast of Florida as Yankeetown (Salmon 1967; Barnwell and Thurman 1984). A sample of crabs collected by Barnwell between these two sites (Econfina River, Taylor County, Florida) remains unidentified. Further field work will be necessary to determine the extent to which the two species overlap geographically.

The processes which led to speciation between these taxa are unknown. A fundamental difference between them is the ability of *U. virens* to withstand colder winter temperature regimes in the northern Gulf of Mexico and the apparent inability of *U. rapax* to acclimate similarly (Miller and Vernberg 1968). If populations were separated on this basis, differences in courtship could have arisen rapidly within the context of intersexual selection (arbitrary female preference for behavior patterns associated with male competition in a different environment; see discussion in Thornhill and Alcock 1983). This hypothesis is consistent with the apparently short period of time in which the two species have been genetically isolated. The fact that displays differ so profoundly between these sibling forms, but no more so than between the cryptic species so far studied (Table 4), confirms that behavioral (and physiological) differences can arise considerably in advance of structural divergence.

Left unanswered is why *U. virens* does not extend farther into southern Florida. Fiddler crabs from all latitudes show only minor differences in upper thermal limits (Vernberg and Tashian 1959). This suggests that the factors limiting the distribution of fiddler crabs within warmer climates are independent of temperature effects, at least at the adult stages. Obviously, further comparative studies are required to obtain answers. In the case of *U. virens* and *U. rapax*, the factors revealed by such an analysis will apparently not be encumbered by the existence of correlated differences in morphology. In that sense, comparative studies between sibling or cryptic species have important advantages (Knowlton 1986).

ACKNOWLEDGMENTS

We are grateful for the continued support over many years from the National Science Foundation. Critical readings by Abby Schwarz, Austin B. Williams and two anonymous reviewers improved the manuscript. This paper is a contribution of the Illinois Marine Biological Association.

LITERATURE CITED

ALTEVOGT, R. 1966. Vibration als semantisches Mittel bei Crustaceen. *Wissenschaftliche Zeitschrift der Karl-Marx-Universitat, Leipzig*. 15:471-477.

_____. 1970. Form und Funktion der vibratorischen Signale von *Uca tangeri* und *Uca inaequalis* (Crustacea, Ocypodidae). *Forma et Functio*. 2:178-187.

BARNWELL, F.H. and C.L. THURMAN II. 1984. Taxonomy and biogeography of the fiddler crabs (Ocypodidae: Genus *Uca*) of the Atlantic and Gulf coasts of eastern North America. *Zoological Journal of the Linnean Society*. 81:23-87.

CHRISTY, J.H. 1978. Adaptive significance of reproductive cycles in the fiddler crab *Uca pugilator*: A hypothesis. *Science*. 199: C.453-455.

_____. 1982. Adaptive significance of semilunar cycles of larval release in fiddler crabs (Genus *Uca*): Test of an hypothesis. *Biological Bulletin*. 163:251-263.

CRANE. J. 1941. Crabs of the genus *Uca* from the west coast of Central America. *Zoologica*. 26:145-208.

_____. 1943. Crabs of the genus *Uca* from Venezuela. *Zoologica*. 28:33-44.

_____. 1975. *Fiddler Crabs of the World*. Princeton University Press. Princeton, New Jersey. 736 pp.

CROZIER, R.H. 1983. Genetics and insect systematics: Retrospect and prospect. pp. 80-92. In E. Highley and R.W. Taylor (eds.) *Australian Systematic Entomology: A Bicentenary Perspective*. CSIRO, Canberra.

FELDER, D.L. 1973. *An Annotated Key to Crabs and Lobsters (Decapoda, Reptantia) from Coastal Waters of the Northwestern Gulf of Mexico*. Center for Wetland Resources, Louisiana State University, Baton Rouge. Publication Number LSU-SG-73-02.

GEORGE, R.W. and D.S. JONES. 1982. A Revision of the Fiddler Crabs of Australia (Ocypodidae: *Uca*). *Records of the Western Australian Museum*. **14(Supplement)**:1-99.

HAGEN, H.O. VON. 1970. Verwandtschaftliche Gruppierung und Verbreitunger karibischen Winkerkrabbe (Ocypodidae, Gattung *Uca*). *Zoologische Mededelingen* (Leiden). 44:217-235.

_____. 1975. Klassifikation und phylogenetische Einordnung der Lautausserungen von Ocypodiden und Grapsiden (Crustacea, Brachyura). *Zeitschrift für Zoologische Systematik und Evolutionsforschung*. 13:300-316.

HALL, J. 1985. Neuroanatomical and neurophysiological aspects of vibrational processing in the central nervous system of semiterrestrial crabs. II. Comparative anatomical and physiological aspects of stimulus processing. *Journal of Comparative Physiology*. A157:91-104.

HUBER, M.E. 1985. Population genetics of eight species of *Trapezia* (Brachyura, Xanthidae), symbionts of corals. *Marine* . 85:23-36.

HYATT, G. 1977. Quantitative analysis of size-dependent variation in the fiddler crab wave display (*Uca pugilator*, Brachyura, Ocypodidae). *Marine Behaviour and Physiology*. 5:19-36.

ICELY, J.D. and D.A. JONES. 1978. Factors affecting the distribution of the genus *Uca* (Crustacea: Ocypodidae) on an East African Shore. *Estuarine and Coastal Marine Science*. 6:315-325.

KETTLER, M.K. and G.S. WHITT. 1986. An apparent progressive and recurrent evolutionary restriction in tissue expression of a gene, the lactate dehydrogenase-C gene, within a family of bony fish (Salmoniformes: Umbridae). *Journal of Molecular Evolution*. 23:95-107.

KNOWLTON, N. 1986. Cryptic and sibling species among the decapod crustacea. *Journal of Crustacean Biology*. 6:356-363.

MACNAE, W. 1968. A general account of the fauna and flora of mangrove swamps and forests in the Indo-West Pacific region. *Advances in Marine Biology*. 6:73-270.

MILLER, D.C. and F.J. VERNBERG. 1968. Some thermal requirements of fiddler crabs of the temperate and tropical zones and their influence on geographic distribution. *American Zoologist*. 8:459-469.

MONTAGUE, C.L. 1980. A natural history of temperate western Atlantic fiddler crabs (Genus *Uca*) with reference to their impact on the salt marsh. *Contributions in Marine Science*. 23:25-55.

NEI, M. 1978. Estimation of heterozygosity and genetic distance from a small number of individuals. *Genetics*. 89:583-590.

RATHBUN. M.J. 1918. The grapsoid crabs of America. *Bulletin of the U.S. National Museum*. 97:1-461.

SALMON, M. 1965. Waving display and sound production in the courtship behavior of *Uca pugilator*, with comparisons to *U. minax* and *U. pugnax*. *Zoologica*. 50:123-149.

_____. 1967. Coastal distribution. display and sound production by Florida fiddler crabs (Genus *Uca*). *Animal Behaviour*. 15:447-459.

_____. 1971. Signal characteristics and acoustic detection by the fiddler crabs, *Uca rapax* and *U. pugilator*. *Physiological Zoology*. 44:210-224.

_____ and S.P. ATSAIDES. 1968a. Behavioral, morphological and ecological evidence for two new species of fiddler crabs (Genus *Uca*) from the Gulf coast of the United States. *Proceedings of the Biological Society of Washington*. 81:275-289.

_____ and _____. 1968b. Visual and acoustical signalling during courtship by fiddler crabs (Genus *Uca*). *American Zoologist*. 8:623-639.

_____, S.D. FERRIS, D. JOHNSTON, G. HYATT and C.S. WHITT. 1979. Behavioral and biochemical evidence for species distinctiveness in the fiddler crabs, *Uca speciosa* and *U. spinicarpa*. *Evolution*. 33:182-191.

_____ and C.W. HYATT. 1979. The development of acoustic display in the fiddler crab *Uca pugilator*, and its hybrids with *Uca panacea*. *Marine Behaviour and Physiology*. 6:197-209.

_____, _____, K. McCARTHY and J.D. COSTLOW, JR. 1978. Display specificity and reproductive isolation in the fiddler crabs, *Uca panacea* and *U. pugilator*. *Zeitschrift für Tierpsychologie*. 48:251-276.

SARICH, V.M. 1977. Rates, sample sizes and the neutrality hypothesis for electrophoresis in evolutionary studies. *Nature*. 265:24-28.

SIEGEL, S. 1956. *Nonparametric Statistics for the Behavioral Sciences*. Mcgraw-Hill, New York. 312 pp.

SELANDER, R.K., W.E. JOHNSON and J.C. AVISE. 1971. Biochemical population genetics of fiddler crabs (*Uca*). *Biological Bulletin*. 141:402.

SULLIVAN, B., K. MILLER, K. SINGLETON, A.G. SCHEER and A.B. WILLIAMS. 1983. Electrophoretic analyses of hemocyanins from four species of mud crabs, genus *Panopeus*, with observations on the ecology of *P. obesus*. *Fishery Bulletin*. 81:883-885.

THORNHILL, R. and J. ALCOCK. 1983. *The Evolution of Insect Mating Systems*. Harvard University Press, Cambridge, MA. 547 pp.

TURNER, K. and T.A. LYERLA. 1980. Electrophoretic variation in sympatric mud crabs from North Inlet, South Carolina. *Biological Bulletin*. 159:418-427.

VERNBERG, F.J. 1959a. Studies on the physiological variation between tropical and temperate zone fiddler crabs of the genus *Uca*. II. Oxygen consumption of whole organisms. *Biological Bulletin*. 117:163-194.

_____. 1959b. Studies on the physiological variation between tropical and temperate zone fiddler crabs of the genus *Uca*. III. The influence of temperature acclimation on oxygen consumption of whole organisms. *Biological Bulletin*. 117:582-593.

_____ and R.E. TASHIAN. 1959. Studies on the physiological variation between tropical and temperate zone fiddler crabs of the genus *Uca*. I. Thermal death limits. *Ecology*. 40:589-593.

WHITT, G.S. 1970. Developmental genetics of the lactate dehydrogenase isozymes of fish. *Journal of Experimental Zoology*. 175:1-36.

WILLIAMS, A.B. 1983. The mud crab, *Panopeus herbstii*, S.L. Partition into six species (Decapoda: Xanthidae). *Fishery Bulletin*. **81**:863-882.

WILSON, F.H., G.S. WHITT and C.L. PROSSER. 1973. Lactate dehydrogenaze isozyme patterns in tissues of temperature-acclimated goldfish (*Carassius auratus* L.). *Comparative Biochemistry and Physiology*. **46B**:105-116.

ZAR, J.H. 1984. *Biostatistical analysis*. Prentice-Hall, Inc. New Jersey. 718 pp.

Contributions in Marine Science. (1987) Vol. 30:77–90.

VARIABILITY IN THE DISTRIBUTION OF LATE-STAGE OYSTER LARVAE IN THE CALCASIEU ESTUARY*

Michael Vecchione[1]

Department of Biological and Environmental Sciences
McNeese State University
Lake Charles, LA 70609

ABSTRACT

The Calcasieu Estuary is the largest body of water in southwest Louisiana and it has been subjected to substantial man-made perturbations. Oyster larvae (*Crassostrea virginica*) were collected in this estuary by net sampling over a four-year period to examine several scales of spatial and temporal variability. The dominant pattern in these data was high variability in replicate collections, perhaps indicating aggregation on a scale of tens of meters. Some patterns were discernible because a large data set was assembled. The highest concentrations of late-stage larvae tended to be near the mouth of the estuary. The larvae were rare in the West Cove area, which is hydrodynamically distinct from the rest of the estuary. Both the eastern part of Calcasieu Lake and the bayous of the upper Calcasieu Estuary appeared to be provided seasonally with a reasonable supply of larval oysters. The strongly bimodal seasonality (spring and autumn) of late-stage oyster larvae may be subject to interannual variability on a scale which is presently unpredictable.

INTRODUCTION

One important aspect of the suitability of oyster (*Crassostrea virginica* Gmelin) habitat is availability of planktonic larval oysters (Cake 1983). Larval oysters are among the most sensitive of estuarine invertebrates to the effects of pollutants (Calabrese and Davis 1966, 1967; Davis and Hidu 1969; Diaz 1971; Calabrese 1972; Roberts, Diaz, Bender, and Huggett 1975; Calabrese, MacInnes, Nelson and Miller 1977; Noyes 1978; Roosenburg, Roderick, Block, Kennedy, Gulland, Vreenegoor, Rosencranz and Collette 1980; Wikfors and Ukeles 1982; Wright, Kennedy, Roosenburg, Castagna and Mihursky 1983). The possibility that entrainment of larval oysters in hydraulic cutterhead dredges could be a substantial source of larval mortality was the impetus for a recent workshop and special publication (Prezant 1986). Furthermore, the

---

* This paper is public domain.

[1] Present Address: National Marine Fisheries Service, Systematics Laboratory, National Museum of Natural History, Washington, DC 20560

planktonic lifestyle of the larvae makes their distribution subject to alterations by changes in estuarine hydrology (Carriker 1951; Pritchard 1953; Kunkle 1957; Wood and Hargis 1971; Seliger, Boggs, Rivkin, Biggley and Aspden 1982; Andrews 1983). Thus, human activities could limit the availability of larval oysters to habitat that is otherwise suitable for oyster production.

The distribution of larval oysters has often been inferred either from gonadal condition of the adult population or from settlement of spat (*e.g.* Haven and Fritz 1985, Kennedy 1986). A more direct, though laborious, method is to sample for the larvae in the plankton (Vecchione 1986). This study is a continuation of a previous project involving the distribution of zooplankton in the Calcasieu Estuary in southwestern Louisiana which has been altered substantially by human activities. Specifically, it was designed to determine patterns of variability in the distribution of late-stage oyster larvae. These patterns include areal, vertical, and temporal variability on several scales.

MATERIALS AND METHODS

Six stations in Calcasieu Pass, Calcasieu Lake, and the Intracoastal Waterway were sampled monthly for 20 months (February 1981-October 1982; Fig. 1). Triplicate samples were collected at all stations with a modified half-meter net with flow meter and 0.153 mm mesh. Sampling at the channel stations consisted of double-oblique, one-minute tows to 3 m depth, while at the shallow lake stations, this gear was towed for one minute just below the surface. At the lake stations (N1, S1 and W1) the stratum very near the bottom was also sampled for 12 of 20 months (May 1981-April 1982) with an epibenthic pullsled, also equipped with 0.153 mm mesh and flow meter (Stubblefield, Lascara and Vecchione 1984). All sampling was scheduled to coincide as closely as possible with daytime high tide to minimize tidal and diel variability. Ancillary data that were collected included water temperature, conductivity, dissolved oxygen, pH and turbidity. Abundances that are presented here are based on calculated numbers of larvae collected per 10 m^3 of water filtered by the net.

As an informal survey of the planktonic molluscs in the area, the molluscs out of one sample from each replicate set were sorted and identified. Larval oysters were found to be occasionally abundant, dominating the bivalve fraction of some samples. As a result of the mesh size used, these were late-stage larvae, mostly Carriker's (1951) "mature" and "eyed" stages. These are the stages which are competent to set within a few days.

The 1981-82 study was designed to eliminate tidal and diel variability; thus it was necessary to assess these components for a complete account of larval distribution. Furthermore, the mollusc data were not collected in replicate and the station coverage did not include the upper estuary. Subsequent sampling was planned for May and August-October, the months when larvae were likely to be present (based on preliminary inspection of the historical data). Station S1, at the south end of the lake, was chosen as the central location for this effort, for integration with other oyster-habitat studies being conducted there at the same time and because inspection of the 1981-82 data also indicated that larvae were likely to be found there.

Ten consecutive one-minute samples were collected at station S1 with the modified half-meter net on 4 August 1983 in order to assess replicate variability. All subsequent sampling was based on triplicate sets because of manpower constraints; the molluscs were sorted and identified from all samples. At each station occupied during this study, standard hydrographic measurements, including temperature, conductivity, dissolved oxygen, pH and secchi depth, were made. At stations that were 1 m or less in depth, hydrographic measurements were made near-surface and near-bottom; where depths were > 1 m, these measurements were made at 1 m intervals from bottom to surface.

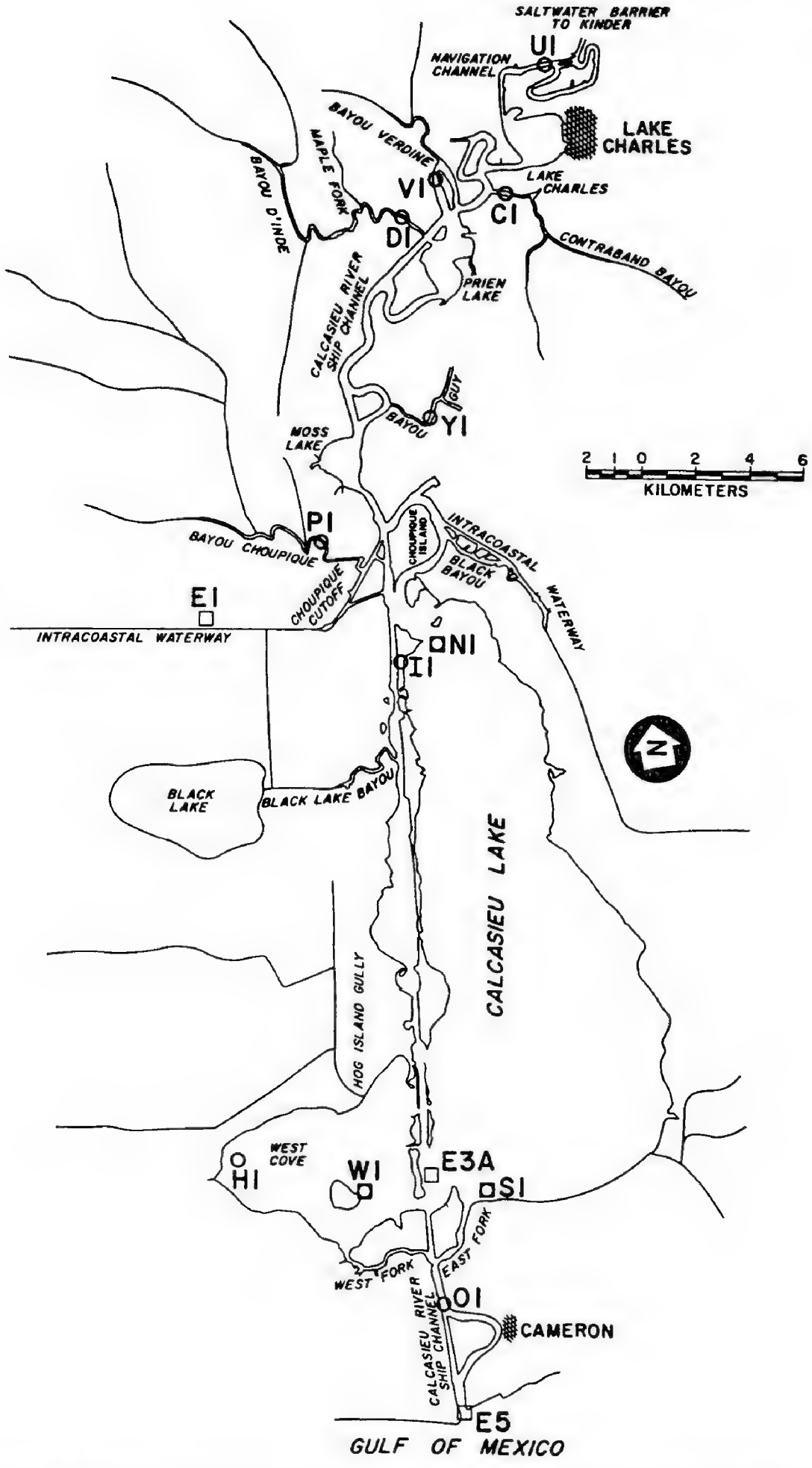


FIG. 1. Sampling stations in the Calcasieu Estuary. Square symbols indicate stations sampled during February 1981-October 1982. Round symbols are stations sampled August 1983-May 1984.

Samples for tidal and diel comparisons both at a fixed station (S1) and within a marked water mass were initially collected on 23 September 1983. Triplicate near-surface and near-bottom

samples were collected at daytime low tide with the modified half-meter net and pullsled, respectively, as described by Stubblefield *et al.* (1984). A windowshade drogue buoy was then released and followed until daytime high tide. Near-surface and near-bottom sampling was conducted, first at the buoy location and again at station S1. The buoy was then followed until nighttime low tide, when sampling was conducted at the buoy location and at station S1. This protocol was duplicated on 28 August 1984.

On 26 October 1983, three bayous in the upper Calcasieu Estuary (stations C1, P1 and D1) were sampled using the modified half-meter net for near-surface tows. The bayous, Contraband, D'Inde and Choupique, were chosen because they are large enough for the sampling methods and because each is subject to a different type of anthropogenic influence. Bayou Contraband flows through the City of Lake Charles and receives treated municipal sewage. The Bayou D'Inde drainage includes a concentration of petrochemical industries. Bayou Choupique is probably the most natural bayou in the estuary and flows primarily through agricultural land and salt marsh.

In order to obtain an overall picture of the areal distribution of larval oysters, stations were sampled throughout the Calcasieu Estuary (all stations except the E-stations) on 24 May 1984, again using the modified half-meter net for triplicate near-surface tows. (Table 1)

RESULTS

Replicate Variability

High variability among replicates was evident throughout this study. In the set of 10 replicates collected in August 1983, oyster larvae were found in only two of the samples. Thus, the coefficient of variation (CV = [standard deviation/mean] × 100) was not calculable until six samples were con-

TABLE 1

Station characteristics.

Station	Type	Depth
E5	Dredged channel	5 m
E1	Dredged channel	3 m
01	Dredged channel	16 m
I1	Dredged channel	16 m
V1	Dredged channel	15 m
U1	Dredged channel	14 m
H1	Lake	1-2 m
W1	Lake	1-2 m
S1	Lake	1-2 m
N1	Lake	1-2 m
P1	Bayou	3 m
D1	Bayou	3 m
C1	Bayou	3 m
Y1	Bayou	1-2 m

sidered. As the sample sizes increased, the CV increased from 246 to 290 at 10 samples. This trend of high variability was consistent among all of the molluscs identified from this sample set but was not true for other taxa such as copepods. Of the 21 sets of triplicate samples that did collect oyster larvae during the field sampling for this project, the average CV was 144 (range = 53 – 173). This value was strongly skewed toward the maximum because 13 of the 21 sets included oyster larvae in two samples each, and only five sets included oyster larvae in all three samples. No relationship was apparent between variability and abundance.

Vertical Distribution

Paired-sample comparisons between the half-meter net and the epibenthic pullsled from the 1981-82 data included seven pairs of samples that collected larval oysters. Based on the Wilcoxon matched-pairs signed-rank test (Siegel 1956), oyster larvae tended to be more abundant in the half-meter net samples (Table 2), but this trend was not statistically significant at the $\alpha = 0.05$ probability level.

Seasonal Distribution

Two peaks in larval abundance were obvious in 1981-82. All of the oyster larvae collected were taken either in May (41%) or in August (6%), September (20%), and October (33%). The August-October peak can be considered

TABLE 2

Comparison of near-surface abundance from modified half-meter net with that of epibenthic pullsled, based on Wilcoxon matched-pairs signed-rank test. Samples collected between May 1981 and April 1982 at stations.N1, S1 and W1.

1/2-m net(A)	Pullsled (B)	A-B	Rank	Signed Rank
1	0	1	1	1
0	23	-23	5	-5
5	0	5	2	2
179	0	I79	6	6
0	18	-18	4	-4
0	9	-9	3	-3
582	0	582	7	7
				W(T) = 4

Non-significant at $\alpha = 0.05$.

to represent late summer-autumn, as only 6% of the larvae were found in August. Although the autumn peak appeared to last longer and to include a larger total percentage of the catch, the spring peak appeared to be more intense.

Areal Distribution

During the months in which oyster larvae were collected in 1981-82, the highest abundances shifted repeatedly among stations (Table 3). Some patterns are evident, however, when the data are pooled. The most obvious trend is a scarcity of oyster larvae in the West Cove area (station W1). Less than 1% of the larvae in the 1981-82 data were collected at station W1 (Table 3). Furthermore, oyster larvae were only found at station W1 during one month, compared with a minimum of three occurrences at each of the other stations. This particularly contrasts with the situation at station N1 at the north end of the lake; whereas abundances were also low at station N1, larvae were collected there in four months. At the remaining stations, both abundances and numbers of occurrences were relatively high. There appeared to be a tendency toward highest larval abundance at the lower end of the Calcasieu Ship Channel (station E5), but when tested against the south end of the lake (station S1) with the Wilcoxon Procedure, the null hypothesis of "no difference" could not be rejected. Thus, the difference in larval abundance between the south end of the ship channel and south end of the lake was not statistically different from random.

The October 1983 samples from the bayous showed that high abundances of larval oysters can indeed be found in the upper Calcasieu Estuary (Table 4).

TABLE 3

Abundance of larval oysters (number collected per 10 m^3 of water filtered) in modified half-meter net samples.

	Station					
Month	E5	S1	E3A	W1	N1	E1
May 1981	977	1	0	0	0	160
August 1981	0	0	0	0	0*	0
September 1981	0	179	147	0	5	166
October 1981	9	582	300	0*	0*	0
May 1982	7	0	0	0	0	0
July 1982	0	0	0	0	0	1
August 1982	171	0	1	0	0	0
September 1982	1	0	5	0	49	0
Percent of Total	42%	27%	16%	0%	2%	12%

* Larval oysters were collected only in the epibenthic pullsled samples.

Consistent differences were evident among the bayous, and when tested with the Kruskal-Wallis non-parametric analysis of variance (Siegel 1956), these differences were found to be statistically significant at an $\alpha = 0.004$ probability level. The differences among bayous in May 1984 (Table 5) were non-significant (at $\alpha = 0.05$), but again the abundance of larval oysters among the bayous was highest in Bayou D'Inde. In the entire system, however, the highest larval abundance in May 1984 was again at the lower end of the ship channel (Station 01).

Small-Scale Spatial and Temporal Variability

The first drogue-buoy experiment was conducted during the autumn larval season. The buoy was released at approximately low tide (1010 CDT, 23

TABLE 4

Abundance of larval oysters (number collected per 10 m^3 of water filtered) in triplicate samples from three bayous in the upper Calcasieu Estuary, October 1983.

Bayou	Station	Sample-1	Sample-2	Sample-3
Choupique	P1	6	2	3
Contraband	C1	1	0	0
D'Inde	D1	23	16	103

TABLE 5

Abundance of larval oysters (number collected per 10 m^3 of water filtered) in triplicate samples from stations located throughout Calcasieu Estuary, May 1984.

Station	Sample-1	Sample-2	Sample-3
O1	73	10	28
I1	4	0	0
V1	0	0	0
U1	0	0	0
H1	2	0	0
W1	6	0	0
S1	0	0	0
N1	0	27	0
P1	0	0	0
D1	0	10	0
C1	0	0	1
Y1	0	0	0

September 1983) after station S1 had been sampled. The wind was blowing from the east at approximately 22.2 km/h (12 kn). Rather than travelling up the lake as would be expected from tidal processes, the buoy moved out toward the old river channel at the south end of the lake. The fact that the buoy was following water movements rather than simply being blown by the wind was confirmed by the arc of a gill net that was found in the area. At about 1300 CDT the wind slacked, and the buoy reversed course shortly thereafter (Fig. 2). Thus, at daytime high tide the buoy had returned to within 0.5 km of its daytime low-tide position. On the outgoing evening tide the buoy tracked straight toward the old river channel, where it finally arrived at nighttime low tide.

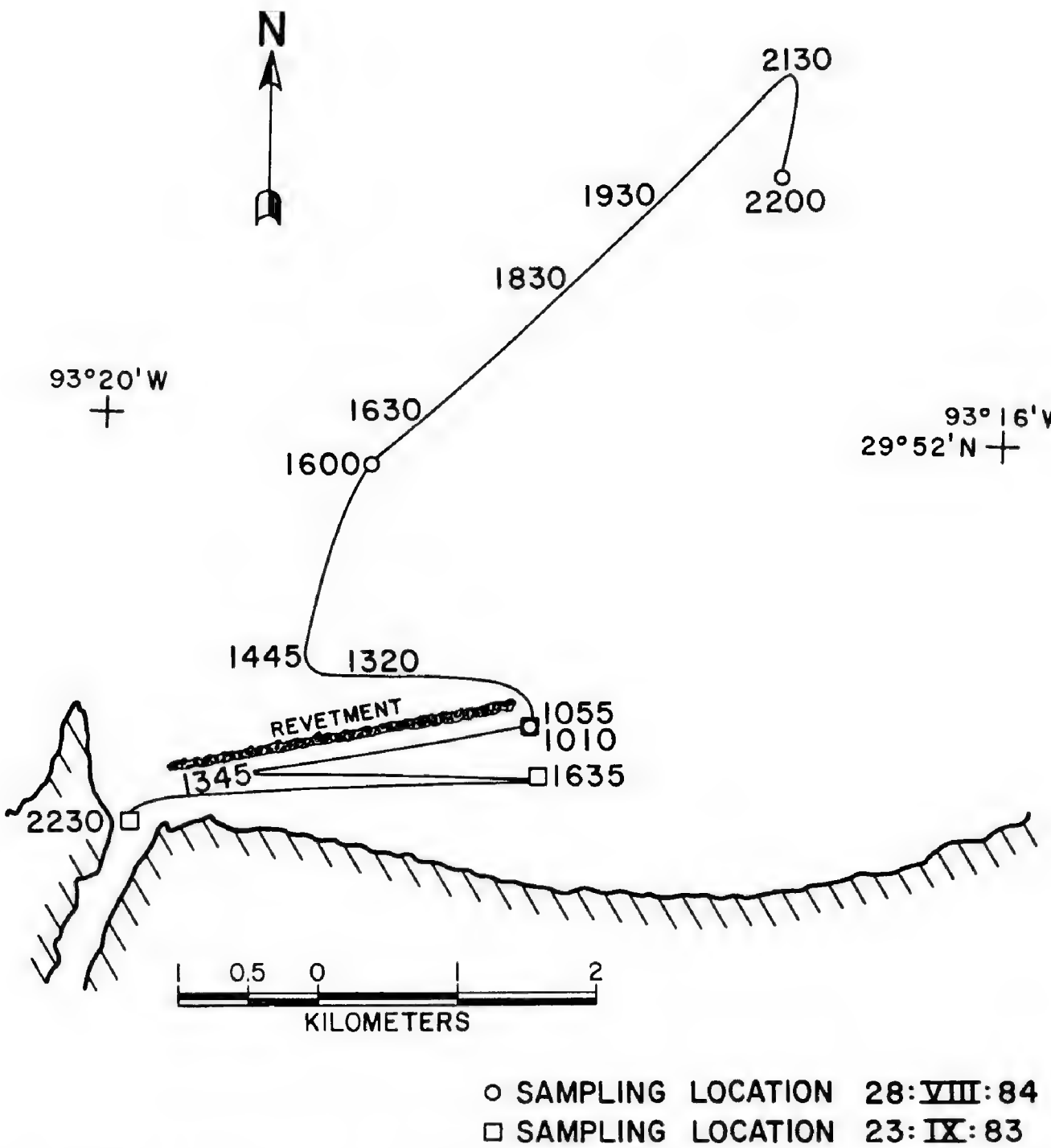


FIG. 2. Paths of a drogue buoy and sampling sites during two comparisons of tidal and diel variability. During sampling, both the buoy location and the fixed station (buoy release point, station S1 in Fig. 1) were sampled.

Although all of the planned samples at the fixed station were collected, difficulties were encountered towing the pullsled at the buoy stations. To function properly, the pullsled must be towed across a bottom that is relatively firm, smooth, and flat. While this was no problem at station S1, sampling wherever the buoy was at the designated sampling time frequently resulted in burial of the pullsled in soft bottom or hanging it on an oyster reef. Thus four near-bottom samples are missing from the buoy sequence (Table 6).

The highest number of samples containing larval oysters came from the initial set of samples, at daytime low tide. The highest recorded abundance, however, was found in the near-bottom samples collected during nighttime low tide at station S1. Abundance near surface was similar between the buoy and fixed station and tended to indicate tidal variability. Conversely, at the fixed station there appeared to be a diel trend in abundance near bottom. The overwhelming trend in the data, however, was for high variability among replicates. Thus, no statistically significant differences could be demonstrated from tidal, diel, vertical, or transport effects.

In August 1984 the pattern of water-mass transport was very different (Fig. 2). On that occasion, wind direction was from the south and the buoy headed up the lake as was expected; however, when the predicted tide changed, the buoy continued up the lake until the south wind slackened at about 2100 CDT. At that time the buoy reversed course and followed the expected tidal drift.

TABLE 6

Comparisons of tidal and diel variability in abundance of oyster larvae (number collected per 10 m^3 of water filtered) both at a fixed station (S1) and in a water mass marked with a drogue buoy.

Date	Diel period	Tide	Gear	Drogue Buoy			Fixed Station		
				Tow-1	Tow-2	Tow-3	Tow-1	Tow-2	Tow-3
Sep 83	Day	Low	1/2-m net	7	10	3	same as buoy		
			pullsled	0	6	0	same as buoy		
	Day	High	1/2-m net	1	0	0	0	1	0
			pullsled	2	0	*	0	5	9
	Night	Low	1/2-m net	0	3	1	0	2	0
			pullsled	*	*	*	70	0	0
Aug 84	Day	Low	1/2-m net	0	0	0	same as buoy		
			pullsled	0	0	0	same as buoy		
	Day	High	1/2-m net	0	0	0	0	0	3
			pullsled	0	0	0	421	14	4
	Night	Low	1/2-m net	11	6	0	38	0	0
			pullsled	0	*	*	*	*	*

* No data collected.

Sampling problems with the pullsled were similar to those described above. In this case, the net was destroyed during retrieval (full of mud) at the buoy location at nighttime low tide. The result was that the only nighttime near-bottom sample was collected at the buoy station. The distributional pattern found in August 1984 contrasted with that of September 1983 (Table 6). No specimens were collected during daytime low tide. The daytime high tide samples from station S1 included both the maximum abundance and the greatest number of samples with larval oysters in these data. Again, however, the high variance among replicates precluded any test of statistical significance of effects.

Interannual Variability

In order adequately to assess changes in abundance among years, it is necessary to develop a biologically meaningful index of annual larval abundance. Either the mean or the median abundance based on the year or on the larval season would indicate uniformly low abundance every year. If, however, the consistently high replicate variability in these data indicates biological patchiness on a very small scale, then perhaps a more meaningful annual index would be an estimate of abundance within these patches. This can be either the maximum recorded abundance or the average of several estimates of abundance within patches (samples with greater than background numbers of larvae). Both of these indices are presented in Table 7. The same pattern is evident in both indices; larval abundance was highest in 1981 and decreased steadily from 1981-1983, and then increased again in 1984. The large decrease in abundance between 1981 and 1982 was primarily because no spring peak was recorded in 1982. Sampling was not done during the spring of 1983 but autumn abundance in 1984 (during the August tidal/diel study) appeared to be higher than that of spring 1984 (during May sampling of the entire estuary).

DISCUSSION

By far, the dominant feature of these data is the high variability on every scale examined. A statistically clumped distribution is indicated when the

TABLE 7

Estimates of interannual variability in larval abundance based on number of larvae collected per 10 m^3 of water filtered.

Year	Maximum abundance	Mean abundance within patches	Standard deviation of abundance within patches	N
1981	977	353	291	8
1982	171	110	86	2
1983	100	65	40	3
1984	420	117	171	5

standard deviation consistently exceeds the mean. The most likely cause of such a distribution is patchiness on a scale smaller than our sampling scale. We used very short (1 min) tows to sample as close to the station as possible, so it appears that the horizontal extent of patches (or as Carriker [1951] referred to them, "larval swarms") of late-stage oyster larvae is in the range of tens of meters or less in the Calcasieu Estuary. Gregarious setting by larval oysters has been well documented (Crisp 1967; Hidu, Valleau and Veitch 1978), but has been assumed to be a response of randomly distributed "searching pediveliger" larvae to concentrated pheromones. These data indicate that the pediveligers may be concentrating in the water column prior to setting, a phenomenon commonly observed in oyster hatcheries (E.W. Cake, Jr., Gulf Coast Research Laboratory, Ocean Springs, MS, personal communications).

A very large data set is required for a true pattern to overcome background 'noise' because of the high replicate variability in these samples. These data may not entirely fulfill this requirement for all of the spatial and temporal patterns addressed. This problem may partly be a result of net sampling for late-stage larvae. These late-stage larvae are comparatively strong swimmers (Carriker 1951, Hidu and Haskin 1978) and differ from the earlier larval stages in behavior (Galtsoff 1964) and distribution (Carriker 1951, Kunkle 1957, Seliger *et al.* 1982). Separate examination of these pre-settlement stages is supported, however, by the lack of correlation in Louisiana between total larval abundance and spatfall (Pollard 1973). Pump sampling and the use of fine mesh nets (0.076 mm or less) would include larvae which may remain planktonic and be further transported for a week or more. Earlier larvae are also subject to varying rates of predation (Burrell and Van Engel 1976, MacKenzie 1977, Steinberg and Kennedy 1979) and other mortality. Unless the larvae are laboriously separated into "stages", inferences cannot be drawn about distribution prior to settlement. The late-stage larvae studied here were within a few days of setting and so they better fulfill the goal of determining habitat suitability (Cake 1983). The trend toward highest abundances in the near-surface samples from the 1981-82 data, though non-significant, did indicate that the half-meter net samples at daytime high tide were sufficiently representative of the abundance of oyster larvae in the water column in the shallow non-stratified areas typical of most of the Calcasieu Estuary.

Some patterns do appear to be indicated by these data. Although larvae were sometimes collected in the West Cove area, they were never common. Hydrodynamic circulation in West Cove is distinct from that of the rest of the Calcasieu Estuary because of West Cove's almost complete isolation by banks of dredged spoil and limited freshwater input. The salinity of West Cove is consistently higher than that of nearby areas in the ship channel and eastern Calcasieu Lake. Ray (1983) monitored spatfall at several locations in West Cove during July-December 1982. He reported spatial and temporal variability with the heaviest set (up to 30 "spat per shell") occurring in August and September. While this is difficult to compare quantitatively with standard measures, such as spat/cm^2 (Pollard 1973; Dugas 1977; Chatry, Dugas and

Easley 1983), Ray's (1983) records of spatfall for West Cove seem light when compared with peaks of 20-65 spat/cm^2 east of the Mississippi Delta (Pollard 1973, Dugas 1977). Low availability of larvae may be contributing to light spatfall in West Cove.

The highest concentrations of larvae tended to be in the lower ship channel. Larval abundance may have been underestimated in the ship channel as only the top 1-3 m of a 13 m water column was sampled. The ship channel is the only part of the ecosystem that is typically stratified, having a halocline at about 3-6 m depth. Net motion in the surface layer of such a system tends to be down-estuary, so larvae collected near the surface in the ship channel would presumably be transported down-estuary if they remained in the surface layer. Since data are lacking on vertical migration in the ship channel and since selective migration of oyster larvae in other systems has been demonstrated (Carriker 1951, Wood and Hargis 1971), it cannot at this time be inferred whether a large percentage of larval oysters are flushed from the Calcasieu Estuary by the ship channel.

Based on published laboratory and field studies, changes in vertical distribution were predicted in response to environmental cues; however, sampling problems and high variability in the data left these expectations without either support or rebuttal. The tracks of the drogue buoy did support earlier proposals (Stubblefield *et al.* 1984, Stubblefield and Vecchione 1985) that the Calcasieu Estuary is primarily wind-driven rather than tide-driven. Thus it seems likely that larvae which are adapted to use tidal currents for favorable transport may be differently affected in this wind-driven system than in the tidal estuaries of the Atlantic coast.

The eastern part of Calcasieu Lake appeared to be provided seasonally with an adequate supply of oyster larvae, especially at the south end of the lake. Similarly, the tidal bayous of the upper estuary probably are regularly "seeded" with larval oysters. The bimodal seasonal pattern (spring and autumn) of larval abundance may be subject to interannual variability or a brief but intense spring peak in 1982 and 1983 may simply have been missed. If the interannual differences noted were real, and not a sampling artifact, the U-shaped pattern over four years may indicate either stochastic changes or a cyclic phenomenon with a period of many years. Confident separation of these alternatives would require several decades of sampling.

ACKNOWLEDGMENTS

I thank Dr. Robert S. Maples for inviting me to participate in the Oyster Habitat project, which was funded by the Office of Coastal Zone Management, Coastal Energy Impact Program grant number NA-83-AA-D-CZ025. I also thank Drs. E. W. Cake, Jr. and Roger Mann for their helpful reviews of earlier drafts of the manuscript. Steve Tramill, Neil Billeaudeaux, Mary Grosze and Cathy Stubblefield all helped with field and laboratory work at one time or another.

LITERATURE CITED

ANDREWS, J.D. 1983. Transport of bivalve larvae in James River, Virginia. *Journal of Shellfish Research.* 3:29-40.

BURRELL, V.G. and W.R. VAN ENGEL. 1976. Predation by and distribution of a ctenophore, *Mnemiopsis leidyi* R. Agassiz, in the York River Estuary. *Estuarine and Coastal Marine Science.* 4:235-242.

CAKE. E.W. 1983. Habitat suitability index models: Gulf of Mexico American oyster. U.S. Fish and Wildlife Service. **FWS/OBS-82/10.57.** 37 p.

CALABRESE, A. 1972. How some pollutants affect embryos and larvae of American oyster and hard-shell clam. *Marine Fisheries Review.* 34:66-77.

CALABRESE, A. and H.C. DAVIS. 1966. The pH tolerance of embryos and larvae of *Mercenaria mercenaria* and *Crassostrea virginica. Biological Bulletin.* 131:427-436.

CALABRESE, A. and H.C. DAVIS. 1967. Effects of "soft" detergents on embryos and larvae of the American oyster (*Crassostrea virginica*). *Proceedings of the National Shellfisheries Association.* 57:11-16.

CALABRESE, A., J.R. MacINNES, D.A. NELSON and J.E. MILLER. 1977. Survival and growth of bivalve larvae under heavy-metal stress. *Marine Biology.* 41:179-184.

CARRIKER, M.R. 1951. Ecological observations on the distribution of oyster larvae in New Jersey estuaries. *Ecological Monographs.* 21:19-38.

CHATRY, M., R.J. DUGAS and K.R. EASLEY. 1983. Optimum salinity regime for oyster production on Louisiana's seed grounds. *Contributions in Marine Science.* 26:81-94.

CRISP, D.J. 1967. Chemical factors inducing settlement in *Crassostrea virginica* (Gmelin). *Journal of Animal Ecology.* 36:329-335.

DAVIS. H.C. and H. HIDU. 1969. Effects of pesticides on embryonic development of clams and oysters and on survival and growth of the larvae. *Fishery Bulletin.* 67:393-404.

DIAZ, R.J. 1971. Effects of thermal shock on larvae of the oyster, *Crassostrea virginica* (Gmelin). M.S. Thesis, University of Virginia.

DUGAS. R.J. 1977. Oyster distribution and density on the productive portion of state seed grounds in southeastern Louisiana. *Louisiana Department of Wildlife and Fisheries, Technical Bulletin.* 23:1-27.

GALTSOFF, P.S. 1964. The American Oyster *Crassostrea virginica* Gmelin. *Fishery Bulletin.* 64:1-480.

HAVEN. D.S. and L.W. FRITZ. 1985. Setting of the American oyster *Crassostrea virginica* in the James River, Virginia, USA: temporal and spatial distribution. *Marine Biology.* 86:271-282.

HIDU, H. and H.H. HASKIN. 1978. Swimming speeds of oyster larvae *Crassostrea virginica* in different salinities and temperatures. *Estuaries.* 1:252-255.

HIDU. H., W.G. VALLEAU and P.P. VEITCH. 1978. Gregarious setting in European and American oysters—response to surface chemistry *vs.* waterborne pheromones. *Proceedings of the National Shellfisheries Association.* 68:11-16.

KENNEDY, V.S. 1986. Expected seasonal presence of *Crassostrea virginica* (Gmelin) larval populations, emphasizing Chesapeake Bay. *American Malacological Bulletin.* Special Edition. 3:25-30.

KUNKLE. D.E. 1957. The vertical distribution of oyster larvae in Delaware Bay. *Proceedings of the National Shellfisheries Association.* 48:90-91.

MacKENZIE. C.L. 1977. Sea anemone predation on larval oysters in Chesapeake Bay (Maryland). *Proceedings of the National Shellfisheries Association.* 67:113-117.

NOYES, G.S. 1978. Effects of petroleum on adults and larvae of the American oyster, *Crassostrea virginica* Gmelin. Ph.D. Dissertation, Rutgers University. 198 p.

POLLARD, J.F. 1973. Experiments to re-establish historical oyster seed grounds and to control the southern oyster drill. *Louisiana Department of Wildlife and Fisheries, Technical Bulletin.* 6:1-82.

PREZANT, R.S. (ed.) 1986. Entrainment of larval oysters. *American Malacological Bulletin.* Special Edition. 3. 74 p.

PRITCHARD, D.W. 1953. Distribution of oyster larvae in relation to hydrographic conditions. *Proceedings of the Gulf and Caribbean Fisheries Institute.* 5:123-132.

RAY, S.M. 1983. Summary Report on Monitoring Program in Lake Calcasieu, Louisiana July-December. 1982. Report to Natural Gas Pipeline Company by Ray Biological Co. 34 p.

ROBERTS, M.H., R.J. DIAZ. M.E. BENDER and R.J. HUGGETT. 1975. Acute toxicity of chlorine to selected estuarine species. *Journal of the Fisheries Research Board of Canada.* 32:2525-2528.

ROOSENBURG, W.H.. J.C. RODERICK, R.M. BLOCK, V.S. KENNEDY, S.R. GULLAND, S.M. VREENEGOOR. A. ROSENCRANZ and C. COLLETTE. 1980. Effects of chlorine-produced oxidants on survival of larvae of the oyster, *Crassostrea virginica. Marine Ecology—Progress Series.* 3:93-96.

SELIGER, H.H., J.R. BOGGS, R.B. RIVKIN, W.H. BIGGLEY and K.R.H. ASPDEN. 1982. The transport of oyster larvae in an estuary. *Marine Biology.* 71:57-72.

SIEGEL, S. 1956. *Nonparametric Statistics for the Behavioral Sciences.* McGraw Hill, New York. 312 pp.

STEINBERG, P.D. and V.S. KENNEDY. 1979. Predation upon *Crassostrea virginica* larvae by two invertebrate species common to Chesapeake Bay oyster bars. *Veliger.* 22:78-84.

STUBBLEFIELD, C.L., C.M. LASCARA and M. VECCHIONE. 1984. Vertical distribution of zooplankton in a shallow turbid estuary. *Contributions in Marine Science.* 27:93-104.

STUBBLEFIELD, C.L. and M. VECCHIONE. 1985. Zooplankton distribution in a wind-driven estuary before and after a major storm. *Contributions in Marine Science.* 28:55-68.

VECCHIONE. M. 1986. The international symposium on the ecology of larval molluscs: introduction and summary. *American Malacological Bulletin.* 4:45-48.

WIKFORS. G.B. and R. UKELES. 1982. Growth and adaptation of estuarine unicellular algae in media with excess copper, cadmium or zinc, and effects of metal-contaminated algal food on *Crassostrea virginica* larvae. *Marine Ecology—Progress Series.* 7:191-206.

WOOD, L. and W.J. HARGIS. 1971. Transport of bivalve larvae in a tidal estuary. pp. 29-44. In D.J. Crisp (ed.) *Fourth European Marine Biology Symposium.* Cambridge University Press. Cambridge.

WRIGHT. D.A., V.S. KENNEDY, W.H. ROOSENBURG, M. CASTAGNA and J.A. MIHURSKY. 1983. Temperature tolerance of embryos and larvae of five bivalve species under simulated power plant entrainment conditions: a synthesis. *Marine Biology.* 77:271-278.

Contributions in Marine Science. (1987) Vol. 30:91–103.

SEM COMPARISON OF FRUITS AND SEEDS OF *SYRINGODIUM* (CYMODOCEACEAE) FROM TEXAS, U.S. VIRGIN ISLANDS, AND THE PHILIPPINES

Louis H. Bragg and Calvin McMillan[1]

Department of Biology
University of Texas
Arlington, Texas 76019

ABSTRACT

Although the congeneric species, *Syringodium filiforme* Kütz. of the Atlantic and *S. isoetifolium* (Aschers.) Dandy of the Indo-Pacific, are vegetatively similar, they can be distinguished on fruit characteristics. After the loss of the fleshy exocarp, the fruit of *S. filiforme* from Texas and the U.S. Virgin Islands has a stony endocarp which tapers in two directions and an apiculate lacinia, but the smaller fruit of *S. isoetifolium* from the Philippines has a rounded base and a blunt-tipped lacinia. In the SEM views, the outer surface of the endocarp of both species is composed of thick-walled cells with irregularly sculptured depressions that are approximately twice as large in *S. filiforme*. The SEM study revealed that the two species are similar in the structure of seed coats and seeds. The embryo of both species is composed of a flattened, oblong hypocotyl with plumule and cotyledon folded into an invagination which lies adjacent to the lacinia in the fruit wall. The flattened fruit of both species is one-seeded and the tan to brown, stony endocarp resembles a shell fragment.

INTRODUCTION

The congeneric species of *Syringodium, S. filiforme* Kütz. of the Atlantic and *S. isoetifolium* (Aschers.) Dandy of the Indo-Pacific, are vegetatively similar; however, they differ, as indicated by den Hartog (1970), in the number of vascular bundles in the leaves and in the size and shape of the fruits. McMillan and Bragg (1987) have noted that den Hartog described fruits with the exocarp intact but that fruits that occur in the sediments lose the fleshy exocarp and retain only the stony endocarp. To determine if further differences in the fruits and seeds could be detected, fruits were examined with scanning electron microscopy (SEM).

Some aspects of floral morphology and development of *Syringodium* have been reported [*S. filiforme,* Tomlinson and Posluszny (1978); *S. isoetifolium*, Lakshmanan and Rajeshwari (1979)], but studies of the fruits have been

[1] Department of Botany, University of Texas, Austin, Texas 78713

limited by the availability of material. Although the SEM comparison is limited to two populations in the Atlantic and one in the Indo-Pacific, as additional collections become available, further assessments can be made.

MATERIALS AND METHODS

Inflorescences were collected from pistillate plants in Texas, U.S. Virgin Islands and the Philippines. Texas fruits were obtained from beach drift in Lower Laguna Madre at Padre Island (26°N, latitude) (Fig. 1). St. Croix fruits were in shallow seagrass beds at Rust-op-twist (17°45'N, latitude) and in Turner Hole (Fig. 1) and Philippine fruits were at Bantayan, Dumaguete City, Negros (9°30'N, latitude). Texas fruits were collected in June 1986 (searches for them were unsuccessful in 1983, 1984, and 1985), St. Croix fruits (Cane Bay) in May 1983 and (Turner Hole) June 1986, and Philippine fruits in July 1983.

The inflorescences were placed in artificial seawater (Instant Ocean), 35‰, at 26-28°C until the fleshy exocarp of the fruits had rotted away from the inner, stony endocarp. The fruits were kept in artificial seawater at 24-27°C until examined with SEM.

For SEM studies, the fruits were treated in the same manner as reported by Bragg and McMillan (1986) for *Halodule*. Fruit walls, seed coats and embryos were dehydrated in an ethanol series through 100% ethanol. No noticeable differences were observed between seagrass fruits and embryos treated in this manner and those kept for 12 h at 24°C in 5% glutaraldehyde in 0.1 M sodium cacodylate buffer (pH 7.2) before dehydration in the ethanol series. Removal of all salt crystals, however, proved to be difficult. Specimens were mounted on double-stick tape and sputter-coated to *ca.* 20-30 nm thickness using a gold target in a Hummer Junior sputter coater. Specimens were examined with a JEOL-35 at 15 kv.

Embryos were studied under light microscopy. The hypocotyls were stained with IKI for starch identification (Berlyn and Miksche, 1976).

The interpretation of the seagrass embryo follows that given by Taylor (1957a, 1957b) for *Zostera marina* L. The storage tissue is interpreted as hypocotyl.

TABLE 1

Fruits of *Syringodium* from Texas, U.S. Virgin Islands and the Philippines[1].

Species and collection site	Length (mm)	mean (mm)	Width (mm)	mean (mm)
S. filiforme[2]				
Lower Laguna Madre, Texas	5.8-7.6	6.2	2.6-2.9	2.8
Cane Bay, St. Croix	5.0-5.9	5.2	2.6-2.9	2.8
Turner Hole, St. Croix	6.0-7.9	6.5	2.0-3.5	2.9
S. isoetifolium				
Dumaguete, Negros	3.8-4.1	4.0	1.9-2.3	2.0

[1] Ten fruits more or less at random were measured for each collection. Measurements are for fruits after the exocarp had rotted away leaving the stony endocarp.

[2] Fruits reported in McMillan (1981) from Lower Laguna Madre ranged from 4.8-7.4 mm in length and 2.0-3.0 mm in width and from Cane Bay, St. Croix from 4.4-6.1 mm in length and 2.5-3.0 mm in width. Florida fruits from Biscayne Bay, Bahia Honda Key and Key West showed the greatest length, 5.2-8.0 mm and width, 2.3-3.2 in that comparison.

RESULTS

Fruit

The fruits of *S. filiforme* and *S. isoetifolium* differed in both size and shape, as indicated by den Hartog (1970). The fruits of *S. filiforme* from Texas and St. Croix were longer and wider than those of *S. isoetifolium* from the Philippines (Table 1). The flattened fruits of *S. filiforme* were *ca.* 1.5 mm thick and those of *S. isoetifolium* were *ca.* 1.0 mm thick. As indicated in Figs. 2 and 3, the fruits of *S. filiforme* are pointed in two directions and those of *S. isoetifolium* are rounded at the base. As indicated in Table 1, the two St. Croix collections differed in size with those from Turner Hole being larger.

The lacinia in the fruit walls differ (Figs. 2, 3, 4, 5). The lacinia of *S. filiforme* is apiculate extending to near the tip of the fruit (Figs. 2, 4), while that of *S. isoetifolium* is blunt-tipped (Figs. 3, 5). The fruits (Figs. 6, 7, 8) of both species

FIG. 1. Inflorescences with mature fruits of *S. filiforme* from the U.S. Virgin Islands and Texas. Fruits have exocarp which was lost before SEM studies. Left: collected on pistillate plants at Turner Hole, St. Croix; right: collected on Padre Island Texas, in beach drift from Lower Laguna Madre. Note differences in internode lengths; those from Texas are approximately 3-4 times longer than those from St. Croix.

FIG. 2. Fruit of *S. filiforme* (Texas) in side view. Scale bar = 1000 μm.

FIG. 3. Fruit of *S. isoetifolium* in side view with outward projection of lacinia. Scale bar = 1000 μm.

have a stylar canal that extends to the inner layer of cells of the fruit wall. The suture line along the lacinia is composed of cells arranged in a matching cascade (Figs. 9, 10). The lacinia at the end opposite the point does not have a suture and remains hinged to the fruit wall (Figs. 2, 3).

The fruit wall of both species is composed of thick-walled endocarp cells with irregularly sculptured depressions on the outer surface (Figs. 11, 12).

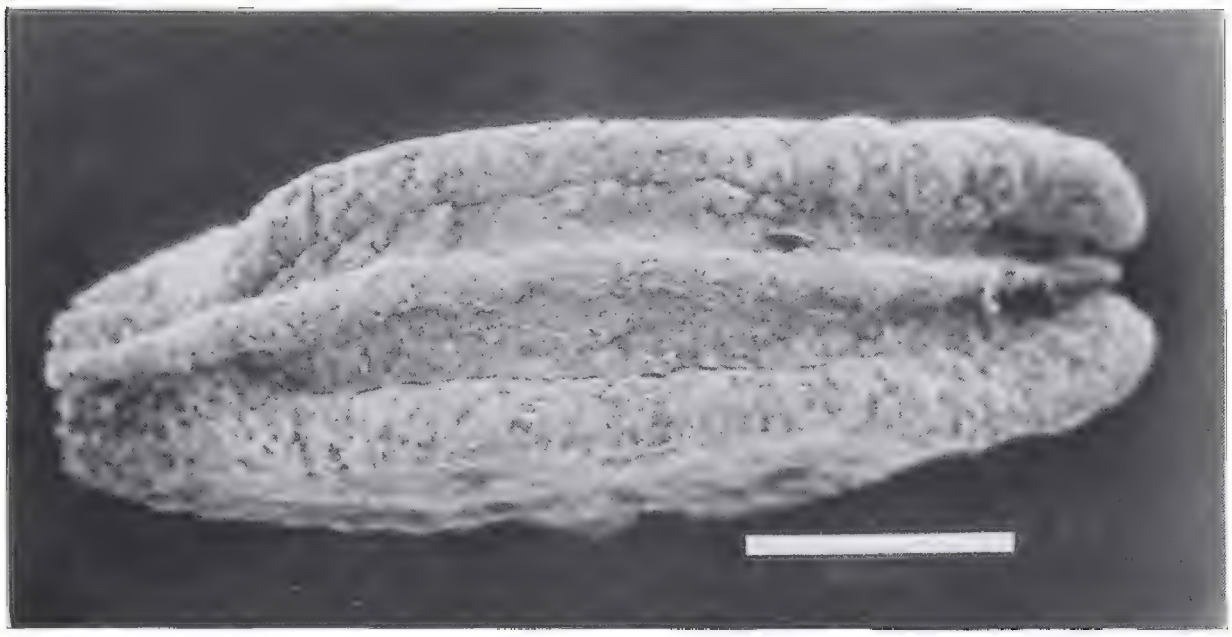


FIG. 4. Fruit of *S. filiforme* (Cane Bay, St. Croix), top view, showing lacinia. Scale bar = 1000 μm.

FIG. 5. Fruit of *S. isoetifolium*, top view, showing lacinia. Scale bar = 1000 μm.

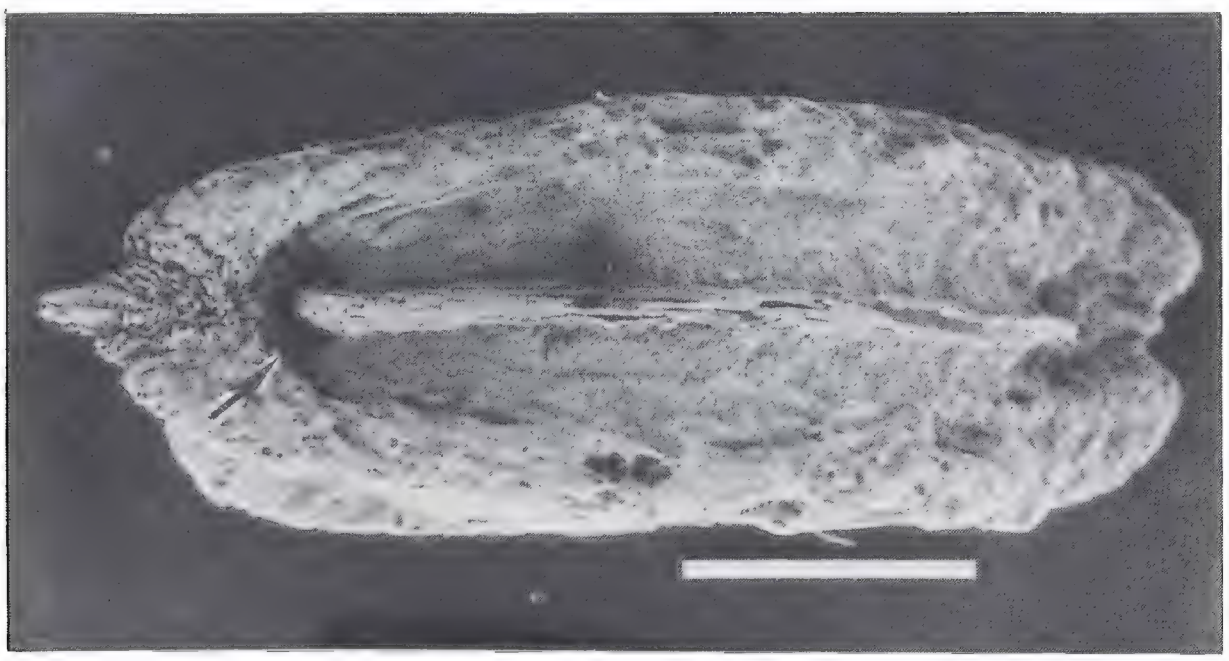


FIG. 6. Lower view of *S. filiforme* (Cane Bay, St. Croix). Stylar end of fruit is to the left. Arrow indicates stylar canal. Scale bar = 1000 μm.

FIG. 7. Longitudinal section of fruit of *S. filiforme* (Cane Bay, St. Croix). Stylar end of fruit is to the left, as in Fig. 6. Arrow indicates the stylar canal. Scale bar = 1000 μm.

FIG. 8. Stylar canal of *S. filiforme* (Cane Bay, St. Croix) fruit with inner surface of endocarp to the right. Arrow indicates stylar canal. Scale bar = 100 μm.

The depressions vary in size and depth, but those of *S. filiforme* (Fig. 11) are approximately twice as large as those of *S. isoetifolium* (Fig. 12). The inner surface of the fruit wall has small, circular depressions that are irregularly distributed (Fig. 13). The endocarp is 7-10 cells thick and composed of cells with multi-layered walls (Figs. 14, 15).

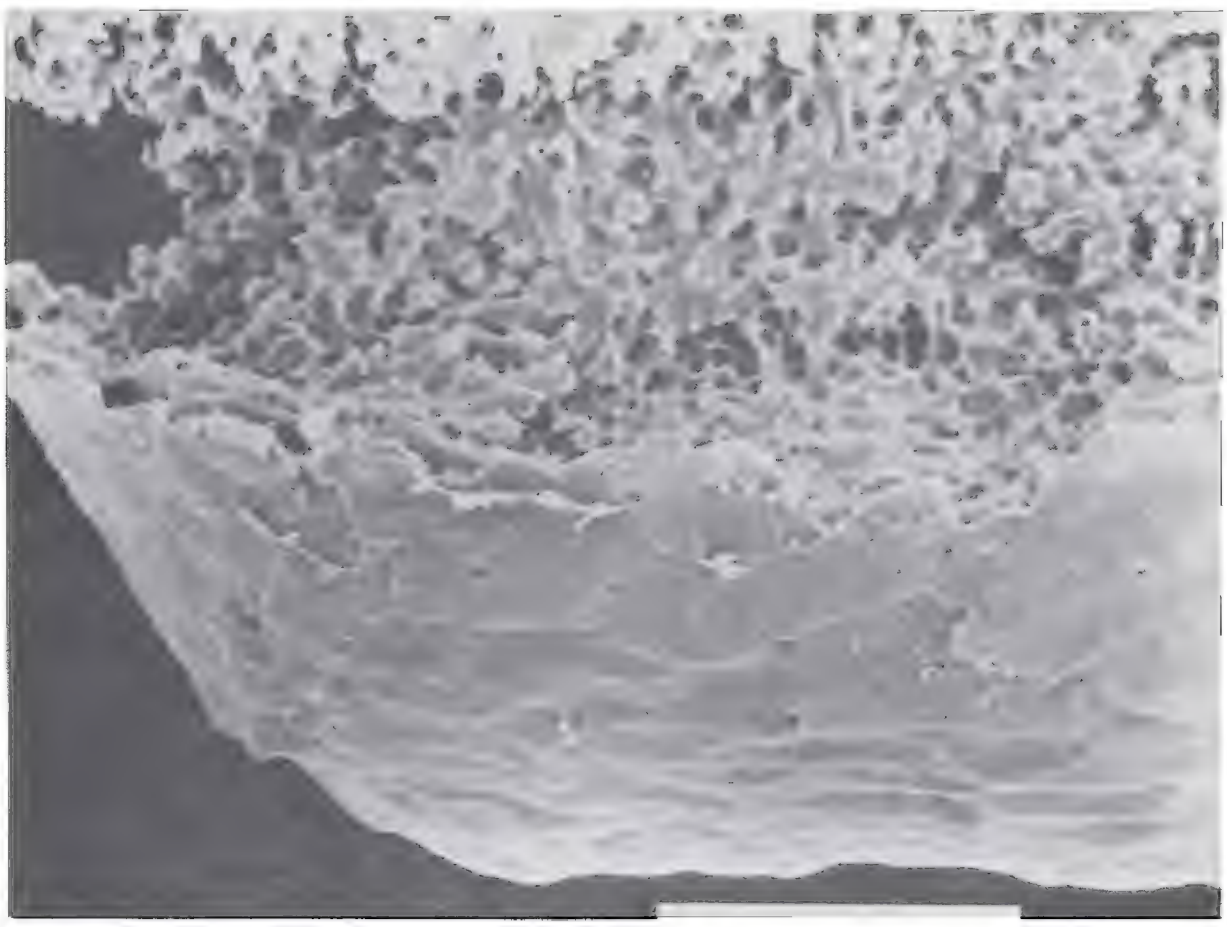


FIG. 9. Side view of lacinia of *S. filiforme* (Cane Bay, St. Croix) showing area adjacent to the tip with the cascade arrangement of cells along the suture line. Scale bar = 100 μm.

FIG. 10. Under side of lacinia of *S. isoetifolium*, showing cascade arrangement of cells along the suture line. Scale bar = 100 μm.

FIG. 11. Outer surface of endocarp, *S. filiforme* (Texas). Scale bar = 100 μm.

FIG. 12. Outer surface of endocarp, *S. isoetifolium*. Scale bar = 100 μm.

Seed Coat

The seed coats of both species are similar in appearance and composed of 5-6 layers of slightly flattened cells (Fig. 16). Toward the stylar end of the fruit, the cells of the seed coat are polygonal.

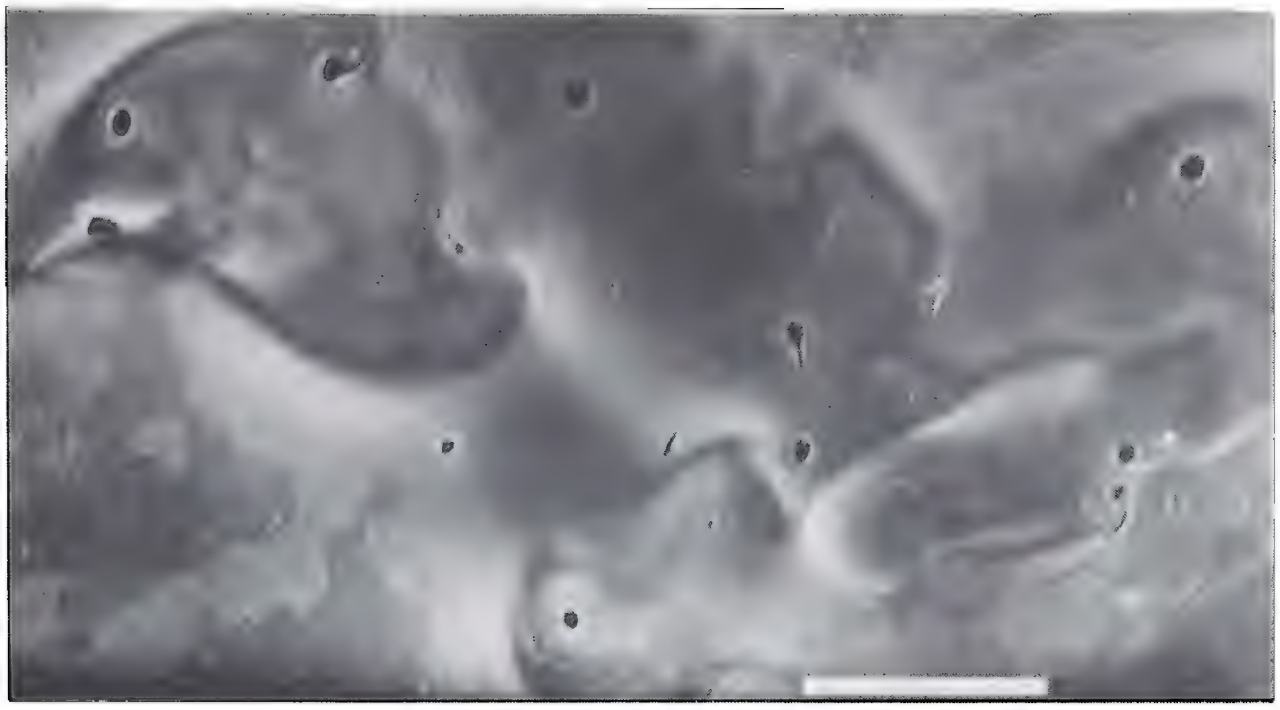


FIG. 13. Inner surface of endocarp, *S. filiforme*, (Cane Bay, St. Croix). Scale bar = 10 μm.

FIG. 14. Cross-section of endocarp of *S. filiforme* (Cane Bay, St. Croix), showing concentrically arranged layers of the cell walls. Scale bar = 10 μm.

Embryo

The embryo of both species is composed of an oblong hypocotyl with a cotyledon folded into an invagination which lies adjacent to the lacinia in the fruit wall. Directly below the point of attachment of the cotyledon are two emergences, differing in size (Fig. 17). The first, and larger, is a dumbbell-shaped section which subsequently gives rise to hairs during germination, and the second, smaller and directly below, is the radicle.

The hypocotyl in both species is composed of uniformly large, polygonal

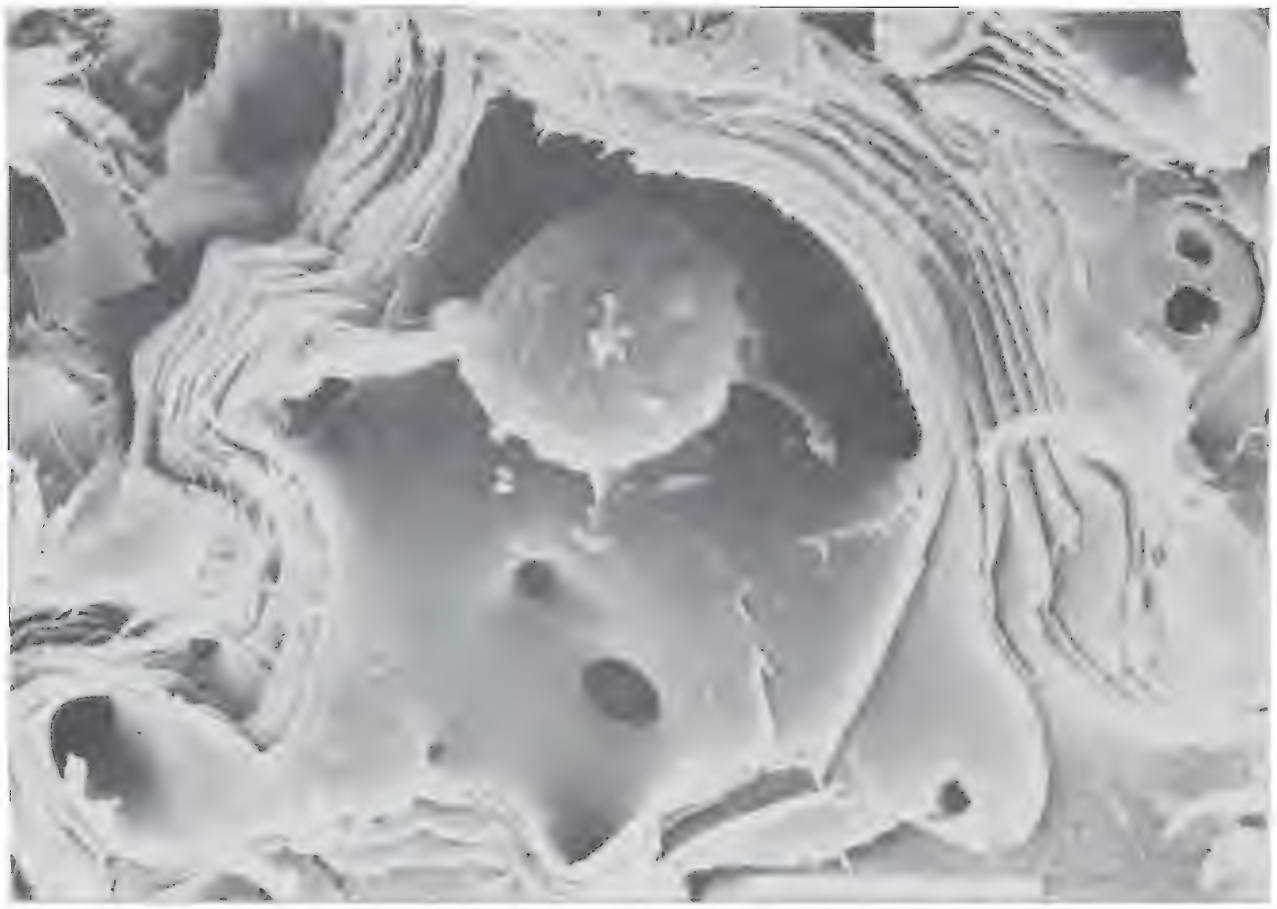


FIG. 15. Cross-section of endocarp of *S. isoetifolium*, showing concentrically arranged layers of the cell walls. Scale bar = 10 μm.

FIG. 16. Section of seed coat showing flattened cells, *S. filiforme* (Cane Bay, St. Croix). Scale bar = 10 μm.

cells. Each cell in the hypocotyl is filled with large starch grains (Fig. 18), as indicated with IKI staining. Cells between the plumule and radicle are smaller than most cells in the hypocotyl.

FIG. 17. Embryo of *S. isoetifolium*, showing arrangement of cotyledon to the left and radicle to the right. Scale bar = 10 μm.

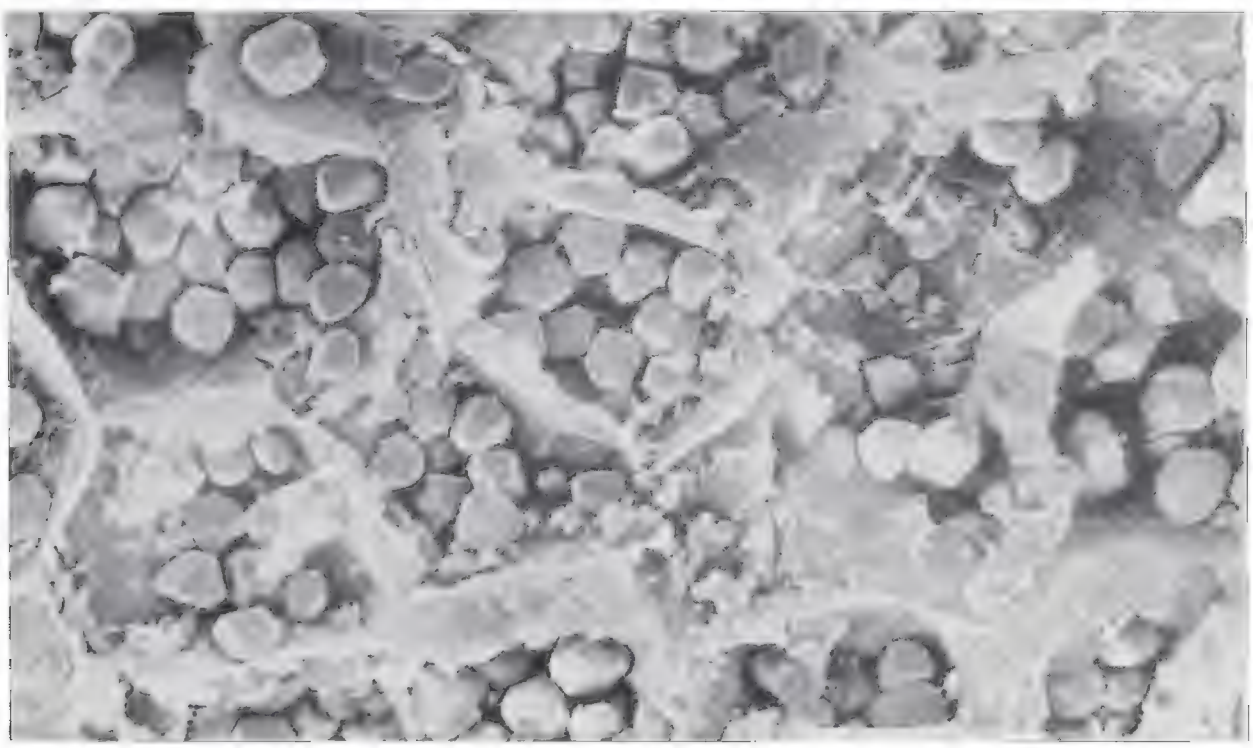


FIG. 18. Hypocotylary cells of *S. filiforme* (Cane Bay, St. Croix), showing starch grains. Scale bar = 100 μm.

The size and shape of the embryos differ and reflect the differences in the fruits. The Texas and St. Croix embryos were *ca* 3.0 mm long and 2.2 mm wide, the Philippine embryo was *ca.* 2.2 mm long and 1.2 mm wide. The embryos of Texas and St. Croix seeds were obovate and those of the Philippines were narrowly oblong.

DISCUSSION

The fruits of *S. filiforme* from Texas and St. Croix were larger than those of *S. isoetifolium* from the Philippines. Den Hartog (1970) had indicated that fruits of *S. filiforme* ranged from 6-7 mm in length and those of *S. isoetifolium* from 3.5-4 mm in length. In the present comparison, fruits collected in Cane Bay, St. Croix, were slightly smaller than those from another bay, Turner Hole. The populational variation within each of the two species should be evaluated as material becomes available.

The fruits of *S. filiforme* from Texas and St. Croix differed slightly in structure from those of *S. isoetifolium* from the Philippines. The lacinia in the fruit wall of *S. filiforme* is apiculate, while that of *S. isoetifolium* is blunt-tipped. The fruit of *S. filiforme* tapers in two directions, but that of *S. isoetifolium* is rounded at the base.

The SEM studies demonstrated a slight difference in the cellular patterns of the fruit walls. For *S. filiforme* from Texas and St. Croix, the sculptured depressions on the fruit wall surface were approximately twice as large as those in the fruit wall of *S. isoetifolium* . The cellular structure of the seed coats and embryos was similar for the fruits from Texas, St. Croix and the Philippines.

Recent SEM studies of fruits and seeds of *Halodule* (Bragg and McMillan, 1986) allow a comparison of two genera in the Cymodoceaceae. The black, rounded fruit of *Halodule* has a suture line which nearly encircles it and is in marked contrast to the tan to brown, flattened fruit of *Syringodium* with a lacinia in the fruit wall that facilitates emergence of the cotyledon. The lacinia in the fruit wall of *Syringodium* is similar to that of *Cymodocea* (McMillan, Bridges, Kock and Falanruw 1982). The fruit wall surface of *Halodule* is composed of interlocking cells, but that of *Syringodium* is composed of thick-walled cells with irregular depressions. In both *Halodule* and *Syringodium*, the endocarp cells have multi-layered walls.

Fruits of *Halodule* and *Syringodium* may remain in marine sediments for an undetermined period of time (McMillan 1981, 1983, 1985) before germination. Seeds of *Halodule* and *S. filiforme* have remained dormant in laboratory cultures for over three years before germinating, but seed germination of *S. isoetifolium* (McMillan, unpublished data 1983-1984) has not been studied for a comparable period of time. The structure of the fruit and seed of *S. isoetifolium*, however, might also permit the "time-capsule" germination that has been reported for *S. filiforme, Halodule wrightii* Aschers., *H. uninervis* (Forsk.) Aschers. and *Cymodocea rotundata* Ehrenb. & Hempr. (McMillan 1981, 1983, unpublished data 1983-85, McMillan *et al.* 1982). The shell-like appearance of the *Syringodium* fruit may offer protection as it remains in the dormant seed reserve of marine sediments.

ACKNOWLEDGMENTS

We thank H.P. Calumpong for the Philippine collection, K.C. Haines and K. Soong for the St. Croix collections and H.J. Arnott for the use of his laboratory

facilities and for his comments on the manuscript. We also thank C. den Hartog and R.C. Phillips for their comments on the manuscript. The SEM studies were conducted in the Electron Microscope Laboratory of the University of Texas at Arlington.

LITERATURE CITED

BERLYN, G.P. and J.P. MIKSCHE. 1976. *Botanical Microtechnique and Cytochemistry*. Iowa State University Press, Ames. 326 p.

BRAGG, L.H. and C. McMILLAN. 1986. SEM comparison of fruits of a seagrass, *Halodule* (Cymodoceaceae), from Australia and Texas. *American Journal of Botany*. 73:815-821.

den HARTOG, C. 1970. *The Sea-Grasses of the World*. North-Holland, Amsterdam. 275 p.

LAKSHMANAN, K.K AND M. RAJESHWARI. 1979. Sea-grasses of Krusadai Island in the Gulf of Mannar, India. II. *Syringodium isoetifolium* (Aschers.) Dandy. *Indian Journal of Botany*. 2:87-95.

McMILLAN, C. 1981. Seed reserves and seed germination for two seagrasses, *Halodule wrightii* and *Syringodium filiforme*, from the Western Atlantic.

_____. 1983. Seed germination in *Halodule wrightii* and *Syringodium filiforme* from Texas and the U.S. Virgin Islands. *Aquatic Botany*. 15:217-220.

_____. 1985. The seed reserve for *Halodule wrightii, Syringodium filiforme* and *Ruppia maritima* in Laguna Madre, Texas. *Contributions in Marine Science*. 28:141-149.

_____ and L.H. BRAGG. 1987. Comparison of fruits of *Syringodium* (Cymodoceaceae) from Texas, the U.S. Virgin Islands and the Philippines. *Aquatic Botany* 28:97-100.

_____, K.W. BRIDGES, R.L. KOCK and M. FALANRUW. 1982. Fruit and seedlings of *Cymodocea rotundata* in Yap, Micronesia. *Aquatic Botany*. 14:99-105.

TAYLOR, A.R.A. 1957a. Studies of the development of *Zostera marina* L. I. The embryo and seed. *Canadian Journal of Botany*. 35:477-499.

_____. 1957b. Studies of the development of *Zostera marina* L. II. Germination and seedling development. *Canadian Journal of Botany*. 35:681-695.

TOMLINSON, P.B. and U. POSLUSZNY. 1978. Aspects of floral morphology and development in the seagrass *Syringodium filiforme* (Cymodoceaceae). *Botanical Gazette*. 139:333-345.

Contributions in Marine Science. (1987) Vol. 30:105–108.

RECURRENCE OF FRUITING BY *HALOPHILA ENGELMANNII* (HYDROCHARITACEAE) IN REDFISH BAY, TEXAS

Calvin McMillan

Department of Botany
The University of Texas at Austin
Austin, Texas 78713

ABSTRACT

Although fruits and seeds of *Halophila engelmannii* Aschers. were described for the first time on material collected in Texas in 1986, fruiting was observed again in Redfish Bay in 1987. Mature fruits were collected in seagrass beds and in beach drift from mid-May through mid-June 1986, but they were collected only in beach drift in mid-June 1987. The low tides and warm water in Redfish Bay in May 1987 preceded the widespread abortion of stems with undeveloped fruit in late May; the high tides, heavy rains and lowered salinity (to 12‰) preceded the appearance of fruits in beach drift in June.

INTRODUCTION

Den Hartog had not observed mature fruits and seeds of *Halophila engelmannii* Aschers. when he published his monograph on seagrasses in 1970. Subsequently he reported (personal communication 1986) that he had not seen any collections of mature fruit until he examined material that was collected in Texas and described for the first time by McMillan (1986). Although McMillan (1985) reported on the frequent production of both staminate and pistillate flowers in late April through mid-June at intervals from 1972 through 1985, the fruits had gone undetected until 1986. The recurrence of fruiting in 1987 may indicate that seed production has been overlooked in previous years.

MATERIALS AND METHODS

Halophila patches in Redfish Bay that had produced mature seed in 1986 (McMillan 1986) were monitored at intervals between October 1986 and June 1987. The observations were made in seagrass beds along the shallow margins of dredge spoil islands near the junction of the Intracoastal Waterway and the Aransas Channel. Some patches were also monitored from March through June in Upper Laguna Madre, also a site of seed production in 1986 (McMillan 1986).

During monthly monitoring for seeds in sediments (McMillan 1987), samples of *Halophila* were examined to determine the phenology in Redfish Bay. Additional samples were examined in Upper Laguna Madre for a comparative phenology.

Fruits of *Halophila* that were collected in beach drift in mid-June 1987 were evaluated for a comparison of size and seed content with material studied in 1986 (McMillan 1986).

RESULTS AND DISCUSSION

Phenology

During the monthly monitoring of *Halophila* patches in Redfish Bay in 1986-1987, no flowers were noted in collections of October through March, but both staminate and pistillate flowers were present in late April. In mid-May, and again, in late May, staminate and pistillate flowers were present and small fruit (1-1.5 mm diameter) contained small immature seeds. On 21 May, many stems with small fruit and immature seeds were in beach drift. Comparable collections in mid-May to late May in 1986 (McMillan 1986) provided mature fruits and seeds. On 16-18 June, 1987, mature fruits were collected in beach drift as they had been on 19 June 1986. In mid-June, no mature fruits were collected in the *Halophila* patches in either 1987 or in 1986.

Staminate flower buds were present in *Halophila* patches in Upper Laguna Madre on 3 April 1987 and floral induction may have been in early March. Sods transplanted from the patches on 19 March and material floated in artificial seawater (Instant Ocean) from the 19 March collection both subsequently had staminate flowers in March in the laboratory. McMillan (1985) reported flower production in March 1975 on transplants to Port Aransas from Redfish Bay in 1974, but no other observations of flower production in March have been noted. Many staminate and pistillate flowers were observed on 1 May in Upper Laguna Madre, but only aborted stems with small fruit and undeveloped seeds were in beach drift on 16 June at the site of collection of mature fruit on 9 June 1986 (McMillan 1986).

Monthly water temperatures in Redfish Bay indicated a relatively mild winter condition (McMillan 1988). A temperature of 29°C in early October 1986 cooled to 20° and 15° in November and December, respectively. Temperatures of 17, 19, 20, and 21°C were recorded in the subsequent four months followed by 29°C in mid-May and 32° in mid-June. Unusually low tides accompanied the warm temperatures of May and these conditions preceded the widespread abortion of fruiting stems with immature fruits which appeared in abundance in beach drift. Heavy rains and high tides with a resultant lowering of salinity to 12‰ on 16 June from 31‰ on 13 May coincided with the appearance of mature fruits in beach drift on 16-18 June.

Although water temperatures and salinities were not monitored from October through June in Upper Laguna Madre, a salinity of 43‰ was recorded in early May. At that time, many staminate flowers were in anthesis. Low tides and high water temperature in May preceded the widespread abortion of fruiting stems with immature fruits as indicated above in Redfish Bay.

Fruits and Seeds

Fruit collected in beach drift along spoil dredge islands of Redfish Bay (Fig. 1) on 18 June 1987 ranged in diameter from 2.5-5.2 mm (Table 1). 80% of

TABLE 1

Size of fruits and number of seeds per fruit for *Halophila englemannii* collected in beach drift in Redfish Bay on 18 June 1987.

No. of seeds/fruit	Percentage of fruits in each diameter (mm) class					
	2.5-2.9	3.0-3.4	3.5-3.9	4.0-4.4	4.5-4.9	5.0-5.2
20			1		1	
19						
18						
17						2
16				1		1
15				1		
14				1	2	
13				2		
12				3	1	1
11				6	2	
10		1	1	3	1	
9			2	1		
8			3	3	4	1
7			1	2		
6		4	3	1		
5		5	4	2	1	
4		7	1	3		
3		4	2	1		
2		4				
1		1	3	1		
0		2	2	1		
Total	3	30	20	30	12	5

the fruits ranged from 3.0-4.5 mm in diameter. McMillan (1986) reported a range of sizes from 3.0-5.5 mm among collections of 20 of the larger fruits measured on 19 and 27 May and 3, 9 and 19 June 1986. As reported by McMillan (1986) the fruits were globose to subglobose with the widest diameter being in the direction of the subtending spathal bracts. The stylar beaks showed a range from 3.0-6.0 mm, as reported by McMillan (1986).

Among 100 fruits floating in beach drift, few still remained attached to stems with a partial pseudowhorl of leaves. Fifty-seven percent had only the subtending spathal bracts and a fragment of the stem attached; 6% had some of the leaves of the pseudowhorl in addition to spathal bracts and 37% were without spathal or leaf attachments.

The number of seeds per fruit ranged from 1-20, as reported by McMillan (1986). Fruits containing seeds included each number except 18 and 19 (Table 1). For the fruits containing seeds, 7.1 was the mean number per fruit.

FIG. 1. Dredge spoil islands in Redfish Bay near the junction of the Intracoastal Waterway and the Aransas Channel. The site of collections of mature fruit of *Halophila engelmannii* in beach drift in 1987 and in both patches and beach drift in 1986.

In addition to mature seeds, various numbers of undeveloped or partially developed ovules were present. In some immature fruits without mature seeds, ovules ranged from 20-29.

The wide diversity of numbers of seeds per fruit reflects the somewhat erratic nature of underwater pollination. Although the pollen grains of *Halophila engelmannii* are produced in linear rows within gelatinous sheaths (McMillan 1985), the actual number of grains which contacts the three stigmas is a variable. Although Cox (1987) contends that pollination in *Halophila* results from pollen propelled in surface rafts with stigmas presenting linear targets at low tide, such a series of events in the pollination of *H. engelmannii* is highly unlikely. Pollination of *H. engelmannii* is likely the result of subsurface movement of pollen grains in sheaths to subsurface stigmatic targets resulting in diverse numbers of seeds per fruit.

LITERATURE CITED

COX, P.A. 1987. Two-dimensional pollination in aquatic angiosperms. *American Journal of Botany*. 74:719.

den HARTOG, C. 1970. *The Sea-Grasses of the World*. North Holland, Amsterdam. 275 pp.

McMILLAN, C. 1985. Staminate flowers and reproductive physiology of *Halophila engelmannii*. *Contributions in Marine Science*. 28:151-159.

_____. 1986. Fruits and seeds of *Halophila engelmannii* (Hydrocharitaceae) in Texas. *Contributions in Marine Science*. 29:1-8.

_____. 1988. The seed reserve of *Halophila engelmannii* (Hydrocharitaceae)in Redfish Bay, Texas. *Aquatic Botany*. (in press).